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## THE RELATION BETWEEN COLOR AND OTHER CHARACTERS IN CERTAIN AVENA CROSSES<sup>1</sup>

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SPECIES crosses among oats have not been studied to any great extent, yet they offer some very interesting problems. Trabut<sup>2</sup> says:

Hybridization between the cultivated species of oats has not yet been methodically attempted to my knowledge, and there is here a very interesting open field. It is true that we have yet to determine in what degree a true hybridization will be possible. If *Avena fatua sativa* may be crossed with *A. sterilis culta*, a progeny may be produced having very useful mixed characters. *A. abyssinica* will gain by being crossed with the really superior *A. strigosa*. But in the matter of hybridization there is much more to be gained from experimentation than from the mere discussion of theoretical views.

Since this paper was read (1911) some studies have been reported on with different species crosses in oats. Zade<sup>3</sup> discusses results obtained from a cross between *fatua* and *sativa*. He found  $F_1$  to be intermediate and that the  $F_2$  gave types resembling *fatua*, *sativa*, and the  $F_1$  intermediate type. These with respect to awns and hairs gave a 1:2:1 ratio.

Surface<sup>4</sup> has described rather fully some results ob-

<sup>1</sup> Paper No. 70, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

<sup>2</sup> *Journal of Heredity*, Vol. 5, pp. 84-85, 1914. (Translated from the original article published 1912.)

<sup>3</sup> *Der Flughofer, Deut. Landw. Gesell. Ab.*, 279: 1-91, 1912.

<sup>4</sup> *Genetics*, Vol. 1, No. 3, pp. 252-286, May, 1916.

tained from a cross between *Avena fatua*  $\times$  *Avena sativa* var. Kherson. The two parent forms differ in a number of characters some of which may be given here. The *Avena fatua* is brown or black in color, has both kernels awned and pubescent and has the typical wild type of base surrounded by a tuft of basal hairs. The Kherson is yellow in color, has few or no awns and lacks pubescence on the glumes and has the typical *sativa* base on which is found an occasional hair.

The  $F_1$  type is intermediate between the two parents. The color of grain is brown but somewhat lighter than the wild parent, and the larger kernel in the spikelet is usually awned,<sup>5</sup> while the smaller or upper kernel is never awned. The lower grain exhibits a medium pubescence while the upper grain is always smooth. The base is intermediate between the two parent forms with tufts of hair on each side but not all around the base.

Some of the results of the  $F_2$  generation may be given in Surface's conclusion:

The data show that the wild parents carry genes for gray and probably for yellow color in addition to the black. These three colors segregate independently of each other. The observed ratio closely approximates the expected and confirms Nilsson-Ehle's conclusions.

The cultivated base of the grain is dominant to the wild and segregates independently of the color genes. The heterozygous condition in the lower grain can be recognized in the majority of plants.

In this cross seven pairs of characters are completely correlated with the character of the base. The characters associated with the wild base are (1) heavy awn on the lower grain, (2) awns on the upper grain, (3) wild base on the upper grain, (4) pubescence on the pedicel on the lower, and (5) on the upper grain, (6) pubescence on all sides of the base of the lower grain and (7) pubescence on the base of the upper grain.

The gene for pubescence on the back of the lower grain is partially linked with the black color factor. The  $F_2$  generation is too small to determine the exact degree of linkage but indicates that there are about 0.7 per cent. of crossovers.

<sup>5</sup> Surface, on page 258 of *Genetics*, Vol. 1, No. 3, 1916, says, "the majority of the lower grains show a weak, straight awn" and on page 265 says "the majority of  $F_1$  spikelets show no awn whatever." It is not clear just which is meant.

The gene for pubescence on the back of the upper grain segregates independently of the color factor except that in the absence of the gene for pubescence on the lower grain the gene for pubescence on the upper is unable to act. In this sense the gene for pubescence on the lower grain is a basic pubescence factor similar to the color factor (C) found in many animals and plants.

#### MATERIAL AND METHODS

The present authors have been working with oat species crosses for several years. A number of different combinations have been made and studied, including several species and many of their derivatives. It is planned here to emphasize certain results obtained with a cross between *Avena fatua* and *Avena sativa* var. Sixty Day. This Sixty Day variety is identical with the Kherson as used by Surface so far as general varietal characteristics are concerned, yet no doubt there are many strains of both sorts.

The *Avena fatua* in appearance was similar to the type used by Surface and has the characters described above. The Sixty Day oat is yellow and seldom do any awns appear. There are no dorsal hairs but an occasional basal hair may be found.

The plants used in making these crosses were grown in the greenhouse since a greater number of successful pollinations can be made than when the plants are grown in the field. The *Avena fatua* was used as the female parent and a number of flowers were emasculated and pollinated. Three seeds developed and each produced a plant. The  $F_1$  generation plants were also grown in the greenhouse since they may receive greater care and more seed may be obtained. All later generations were grown in the field, spacing the plants two to three inches in the rows.

#### DISCUSSION OF RESULTS

The  $F_1$  type was as described by Surface, generally intermediate in type. The color was brown somewhat lighter than the wild type. The large kernel of the spikelet was often awned and was covered with dorsal

hairs. The small kernel of the spikelet was never awned but had an occasional sprinkling of dorsal hairs. The base was more like the *sativa* type, yet appeared to be more intermediate in type with some basal hairs on either side of the base but not at the back.

When the seeds from the first generation plants were sown, a number of different types appeared in the second generation. There were some that resembled the two parent forms and also other types different in color, amount of awning, pubescence, and the like.

As regards color there appeared four types, black, gray, yellow and white. The white ones, of which there were only four, were tested later and proved to be gray, thus leaving only the three color types. The black oats were of two general types, those having the two strong awns and pubescence on both kernels and the wild base, and those having pubescence on the large kernel and sometimes on the small one and with an intermediate or *sativa* type of base. Some of these forms were awnless and others possessed varying amounts of awn which were in some cases strong and in others weak.

The gray colored oats were both pubescent and smooth, some fully awned, some partially awned, and some awnless. They also segregated as to type of base.

The yellow oats, however, were all smooth and possessed very few or no awns. No yellow oats developed the strong awns similar to the wild type.

The segregation as to color and percentage of awns of the second generation plants is shown in Table I.

TABLE I  
SHOWING THE SEGREGATION AS TO COLOR AND PERCENTAGE OF AWNS. SERIES  
687, *Avena fatua* × *Avena sativa* VAR. SIXTY DAY  
*Percentage of Awns*

Color	0	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100	Totals
Black . . . .	46	25	20	23	12	17	21	23	14	8	2	99	310
Gray . . . . .	11	9	6	10	3	10	6	5	1	3		28	92
Yellow . . . .	9	7	1	1									18
Totals . . . .	66	41	27	34	15	27	27	28	15	11	2	127	420



The percentage of awns was determined by taking a typical head from each plant and counting the total number of spikelets and the number of awned spikelets, and then determining the percentage of awned spikelets. Since there are a number of plants having no awns and also a number having 100 per cent. it seems best to arrange the classes as has been done in this table; that is, separate classes have been made for the 0 and 100 per cent. values.

From this table it is clear that the black oats possessed varying degrees of the awned condition from awnless to fully awned. The grays too showed about the same range of distribution. The yellow types, however, showed a tendency to be grouped in the lower classes. No yellow types were found having more than 30 per cent. of awns. It seems quite evident that there may be some relation between the yellow oat and the lack of awning.

Nilsson-Ehle<sup>6</sup> has discussed a case of a cross in oats where there was an apparent inhibition of awning produced by a yellow oat. He concludes that there was some inhibitory effect of the yellow color or that the yellow color factor acted also as an inhibitor of awns. The oats Nilsson-Ehle worked with were domestic types and it is a well-known fact that the domestic sorts vary as to the amount of awns with the change in environment. For that reason it is felt that results obtained from wild crosses will be more definite since the wild type produces its fully awned condition under very diverse growth conditions. This is all the more evident from a cross of this same Sixty Day type used in these crosses with a black cultivated oat. It was found that the yellow oats segregating from this cross contained fewer awns than did the blacks, whites, and grays but that the percentage of awns on the black parent was so variable that the results obtained are not definite. Such is not the case for the awning of the *Avena fatua* as stated above.

<sup>6</sup> Zeitschrift für induktive Abstammungs- und Vererbungslehre, Bd. XII, Heft 1, 1914.

These results show that the segregation as to color, as mentioned above, produces three types, black, gray and yellow. On the assumption that the wild oat carries genes for black, gray and yellow we would expect a segregation of 12 black : 3 gray : 1 yellow. These figures approach this result, but there are too few yellows and too many grays. Instead of the numbers obtained we expect 315.00 blacks:78.75 grays:26.25 yellows. It is very difficult to always distinguish between pale grays, yellows and whites, a fact which is well known to those working with oats. This is especially true in unfavorable seasons when oats are likely to weather badly. No doubt this difficulty is one of the reasons for the deviation of the gray and yellow classes. When we group the non-blacks together we have a very fair approximation to the 3:1 ratio, which ratio would be expected on the above assumption.

The relation between color and pubescence for these same second generation plants is well illustrated by Table II.

TABLE II

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE OF THE SECOND GENERATION PLANTS OF SERIES 687, *Avena fatua* × *Avena sativa*  
VAR. SIXTY DAY

*Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black.....	112	198		310
Gray.....	26	42	24	92
Yellow.....			18	18
Totals.....	138	240	42	420

Certain interesting facts are brought out by this table. It is apparent that all of the black oats are pubescent, some having both kernels pubescent and a larger number having only the one kernel pubescent. It is very significant that there are no smooth black oats. The gray oats, on the other hand, have a certain number of which both kernels are pubescent, a larger number with one

kernel pubescent, and still another lot of smooth oats. It seems that the gray oats segregate as to pubescence on what may be a 1:2:1 ratio. Regarding the yellow oat it is very significant that all of them are in the smooth class. That is, no yellow oats are found which are pubescent. Certain ones which were found appeared yellow but which proved on testing to be gray instead of yellow, so that at present no true yellow oats which are pubescent have been obtained out of this cross.

From these data it seems without any doubt that yellow oats in some way or another tend to inhibit the factor for pubescent. It is also apparent that there is one factor for pubescence which is linked with the black color factor. There seems to be another factor for pubescence which is independent of any color factor and for this reason we obtain gray oats in approximately the ratio of 1:2:1 so far as pubescence is concerned. Owing to the inhibiting effect of the yellow oat, there are no pubescent forms obtained. From this material it is clear then that we are working with a *fatua* form which has two factors for pubescence, one of which is linked with the black color factor and one which is independent. More will be said regarding these facts later in this paper, when another cross will be mentioned.

Another interesting relationship is that shown between the color in the  $F_2$  generation and the segregation as to type of base. As mentioned earlier in this paper, the type of base differs from the wild form which is the typical sucker-mouth shape while that of the cultivated oat is of the typical *sativa* form. The *sativa*-like form is dominant or partially so to the wild type. A study of this and a large number of other crosses in which the wild type has been used as one of the parents indicates that the segregation of the base follows the 1:3 ratio, wild being the recessive type.

The relation between color and type of base for the second generation plants of this cross is shown in Table III.

TABLE III

SHOWING THE SEGREGATION AS TO COLOR AND TYPE OF BASE. SERIES 687.  
*Avena fatua* × *Avena sativa* VAR. SIXTY DAY

## Type of Base

Color	Wild	Sativa	Totals
Black .....	97	213	310
Gray .....	26	66	92
Yellow .....		18	18
Totals .....	123	297	420

From this table it is clear that the black oats segregates into the wild and *sativa* forms as also do the grays. On the other hand, the yellow oats exhibit no wild type of base but are all of the *sativa* class. It is also apparent from these data, then, that in addition to the inhibition of awn production and pubescence there is also some factor or factors which inhibit the production of the wild type of base when this particular cross is made. That it must be due to some factor or factors related to the yellow oats is clear from the fact that with a large number of crosses in which white oats and other forms have been used, the grays and whites as well as the blacks exhibit the wild type of base in about the ratio that would be expected.

TABLE IV

SHOWING THE RELATION BETWEEN COLOR AND PERCENTAGE OF AWNS FOR THE  
 THIRD GENERATION FAMILIES PRODUCED FROM THREE HETERO-  
 ZYGOUS PLANTS OF THE SECOND GENERATION. SERIES  
 687. *Avena fatua* × *Avena sativa* VAR.  
 SIXTY DAY

## Percentage of Awns

Color	0	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100	Totals
Black ....	82	45	17	9	3	4	5	3	4			58	230
Gray .....	12	13	6	1	2	1	2	1		1		18	57
Yellow ...	10	7	2			1	1						21
Totals ..	104	65	25	10	5	6	8	4	4	1		76	308

Seed from a large number of  $F_2$  plants were tested in the  $F_3$  generation but all of these will not be discussed here. Three of these which exhibited the segregation

similar to that obtained in the  $F_2$  generation have been brought together and the results are here shown for the three classifications made on the second generation.

The relation between color and percentage of awns of these three families mentioned above is shown in Table IV.

Here again, it is apparent that the black oats ranged all the way from awnless to 100 per cent. awns as do the gray oats. The yellow oats, on the other hand, are grouped near the lower percentage classes. Two individuals, however, exhibited about 50 per cent. of awns, one being in class 40 to 49, one in 50 to 59. It may be that these will be found to be grays instead of yellows. However, in general, the tendency is for the yellows to exhibit only a few awns. This is in accordance with the results obtained on the second generation and substantiates the conclusion drawn from the study of that material. It may be worth while to call attention here to the segregation as to color which fits the hypothesis more closely than does the material of the second generation. The segregation exhibits what is without doubt a 12:3:1 ratio. The observed numbers are 230 black: 57 gray:21 yellows while the expected numbers are 231.00 blacks : 57.75 grays : 19.25 yellows.

The relation between color and pubescence on these third generation families is shown by Table V.

TABLE V

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE OF THREE  $F_3$  FAMILIES GROWN FROM HETEROZYGOUS  $F_2$  PLANTS. SERIES 687

*Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black.....	91	139	—	230
Gray.....	19	12	26	57
Yellow.....	—	5	16	21
Totals.....	110	156	42	308

Here it is clear that again all the black oats are pubescent while the gray oats fall into the three classes. The

segregation of the grays does not follow the 1:2:1 ratio here but it is possible that some of those classed as non-pubescent may have a few hairs when examined more closely. It was found with the second generation material that it was necessary to use a lens with certain ones, especially where there was very little pubescence showing. This has not been done with all those in this table and, therefore, it is possible on later examination that some of them may fall into the group of one kernel pubescent. The yellow oats also, instead of all being in the non-pubescent group, have a few in the class having one kernel pubescent. It is likely that on later examination these will be found to be gray oats. This can not be said at present. In general, it may be said that this segregation agrees very closely with that of the second generation with the exception of the five yellow plants which seem to exhibit some slight amount of pubescence.

The relations between color and type of base for these same three third generation families is shown in Table VI.

TABLE VI  
SHOWING THE RELATION BETWEEN COLOR AND TYPE OF BASE IN THREE THIRD  
GENERATION FAMILIES. SERIES 687, *Avena fatua* × *Avena sativa*  
VAR. SIXTY DAY

*Type of Base*

Color	Wild	Sativa	Totals
Black .....	57	173	230
Gray .....	18	39	57
Yellow .....		21	21
Totals .....	75	233	308

On examining this table it is clear that the segregation of these third generation families agrees very closely with that of the second generation material. The black and gray oats have both wild and *sativa* bases in apparently a 1:3 ratio. The yellow oats, on the other hand, have only the *sativa* base. This material tends to substantiate the conclusions drawn from the second generation material, which is to the effect that it does not seem

possible to produce a yellow oat from this cross having the type of base of the wild parent.

Further information may be had regarding pubescence and color on examining the results on three other third generation families which have been grouped according to color and pubescence. The parent plants which produced these three families were black, pubescent on one kernel and nearly awnless.

These results are shown in Table VII.

TABLE VII

SHOWING THE RELATION BETWEEN COLOR AND PUBESCENCE FROM THREE  
THIRD GENERATION FAMILIES OF SERIES 687, *Avena fatua* ×  
*Avena sativa* VAR. SIXTY DAY

*Pubescence*

Color	One Kernel Pubescent	Smooth	Totals
Black .....	231		231
Yellow .....		88	88
Totals .....	231	88	319

The segregation shows that no gray was present and that the segregation is only for blacks and yellows so far as color is concerned and follows an approximate 3:1 ratio. In regard to the pubescence it is clear that all of the black oats are pubescent while all the non-blacks or yellows are smooth. This material further substantiates the statement made earlier in this discussion to the effect that there is a pubescent factor linked with the black oat.

## GENERAL DISCUSSION

The foregoing data show that there is a very definite relation between color of glume and production of awns. On the black and gray oats awns are produced in varying amounts while few or no awns are produced on the yellow oats. Regarding the inheritance of awns, it has been shown<sup>7</sup> that the weak awn is inherited on a 1:3 ratio, the fully awned condition being recessive. The data

<sup>7</sup> Love, H. H., and Fraser, A. C., "The Inheritance of the Weak Awn in Certain *Avena* Crosses," AMER. NAT., 51, No. 608, August, 1917.

that have already been collected show also that the strong awn is inherited in the same manner. These data (Tables I and IV) give 203 fully awned : 525 partially awned or awnless, giving 2.92:1.12 per 4. We would expect on a 1:3 basis 182:546. The action of the yellow factor is to reduce the amount of awns on the yellow glumed oats.

It was stated earlier that there was apparently a pubescence factor linked with the black and also another pubescence factor which was not linked with any color. If this were true and there was no inhibitory effect produced by the yellow oats we would expect to obtain 15 pubescent to 1 non-pubescent form in the second generation. It may be well to state here that it has been found by experiment that the wild form used in this cross was of such a type that it had two factors for pubescence. We have also found another form which has only one factor for pubescence. When this form is crossed with a white oat, all of the non-blacks are smooth, showing that this form has the pubescence factor which is linked with the black while the forms having the two factors for pubescence give both pubescent and smooth non-blacks. This is well brought out by the data presented in Table VIII. Here the same white sort, Tartar King, was crossed with two forms of *Avena fatua*.

This table is made up of data of the second generation. It is possible that later experimentation may change the relationship of the colors particularly so far as the grays and whites are concerned. In these tables all those not showing blacks and grays are classed as yellows and whites. The further study of these has not proceeded far enough to determine just the relation here. It seems, without doubt, that we have two types of *fatua*, one giving the 15:1 ratio (Series 351a1) and one the 3:1 (Series 351b1). Again in the 3:1 distribution all the non-blacks are smooth.

It will be of interest here also to state when the type having one factor for pubescence was crossed with the Sixty Day type similar to the one used in Series 687 that all of the non-blacks, both grays and yellows, were



TABLE VIII

SHOWING THE SEGREGATION AS TO COLOR AND PUBESCENCE ON A CROSS BETWEEN *Avena fatua* and *Avena sativa*, VAR. TARTAR KING

Series 351a1

*Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black .....	30	74		104
Gray .....	9	19	3	31
White and yellow .....	3	3	5	11
Totals .....	42	96	8	146
	138		8	

Series 351b1

*Pubescence*

Color	Both Kernels Pubescent	One Kernel Pubescent	Smooth	Totals
Black .....	72	144		216
Gray .....			61	61
White and yellow .....			18	18
Totals .....	72	144	79	295
	216		79	

smooth, showing that this form has the pubescence factor closely linked with the black color gene.

The results as obtained from Series 687 so far as color and pubescence are concerned may be explained in the following manner. We may assume the *Avena fatua* to be represented by BBGGYYPP, that is, possessing the factors black (B) which also produces pubescence, gray (G), yellow (Y) and another factor (P) for pubescence. The Sixty Day oat then may be bbggYYpp. We then assume Y to inhibit the production of pubescence in the absence of B or G.

It may also be well to state that the results here found can also be explained by assuming Y to have the effect of producing pubescence in the presence of G. We would then not assume any pubescence factor (P) for this explanation. This assumption would account for the results as well as the one chosen. On the other hand, from data already obtained on other crosses it does not

seem that this latter explanation is the one which should be used.

On the first hypothesis the  $F_1$  individuals are, therefore, BbGgYYPp forming eight kinds of gametes. From this assumption then we would expect 48 black pubescent:9 gray pubescent:3 gray smooth:4 yellow smooth. The ratio of pubescent to non-pubescent would be 57:7. The observed numbers in the second generation were 378 pubescent : 42 smooth. We would expect 374.06 pubescent : 45.94 smooth. The observed numbers from the three third generation families gave 266 pubescent : 42 smooth, while we would expect 274.31:33.69. Considering the two groups together we have 644 pubescent:84 smooth, while we would expect 648,375:79.625. We see that the observed facts agree very well with the theory.

While it is not intended to go into details regarding the  $F_3$  generation, it may be said that a number of observed facts tend to substantiate this hypothesis. For example, we should have some families segregating in the third generation giving 15 pubescent : 1 smooth. This we find to be so. Again we would, according to theory, expect to find some  $F_3$  families segregating into blacks and grays where the grays would all be smooth. This we find also. We would also expect some gray oats to segregate into 9 pubescent : 7 smooth. This combination has also been found.

Regarding the base, it might be well to state that in studying the segregation of this series into the third and even into the fourth generation as yet no yellow oat has been found exhibiting the wild type of base. These results do not agree with those obtained by Surface although in general we might expect them to be similar since the yellow Sixty Day oat and the Kherson type are classed by some as the same variety of oat. Yet when we know that it is possible to obtain different strains out of a variety, particularly so far as the inheritance is concerned, it is not surprising that these results should not agree. Let us illustrate this by some results we have

obtained from crossing two black oats which by those studying classification of varieties of oats have been classed as the same variety and exhibit the same general botanical characters. When these two forms were crossed, both being black, the first generation plants were black but when the second generation was grown it was found that a segregation was obtained, giving 15 black to 1 non-black. This point then illustrates the statement made above that we shall probably obtain different segregations even though we are supposed to be using the same variety. This is also brought out by the fact that from the wild form, *Avena fatua*, we have been able to obtain different types so far as pubescence is concerned. How many other types may exist in the wild form of *fatua* we do not know, but experiments are underway to determine whether it is not possible to find other types as regards color and certain other characteristics.

From what is here said we do not intend to convey the idea that yellow color as found in oats will inhibit the production of awns, pubescence and base but mean merely that the yellow as exhibited in this series does that. In fact, we know from the crosses we have already studied where other yellow forms have been used that it is possible to obtain the yellow pubescent form and yellow ones with the wild base. Therefore, the statements made here hold only for the particular cross here reported.

#### CONCLUSION

The studies here presented show that we have some relation between these yellow oats and the absence of awns, pubescence, and the wild base. We also find that there are two types of pubescence, or better stated, two factors for pubescence, one of which is linked with black and one which is independent of any color factor. Owing to the inhibitory effect, we do not get a definite Mendelian ratio from these studies. It is also clear that the third generation material tends to substantiate the conclusion arrived at from the study of the second generation plants.

## STUDIES IN PALEOPATHOLOGY.

### III. OPISTHOTONUS AND ALLIED PHENOMENA AMONG FOSSIL VERTEBRATES

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EVERY student of the fossil vertebrates who is fortunate enough to collect a number of complete or approximately complete skeletons of fossil vertebrates is almost sure to be impressed with the frequency of the peculiar curve to the backwardly bent neck and the rigid appearance of the limbs, if these members are preserved in anything like the position assumed by the animal at death. This attitude of the skeleton is very common in the petrified remains of extinct animals and it is doubtless what is known to medical men as opisthotonos. Williston<sup>1</sup> in describing the remains of *Cimoliosaurus Snowii*, a long-necked plesiosaur, from the Cretaceous of Kansas, says:

The specimen comprises the skull and twenty-eight cervical vertebræ, all attached and with their relative positions but little disturbed. They lie upon the right side, with the usual opisthotonic curve to the neck, and are all laterally compressed.

The attitude has been noted among many other fossil vertebrates, but its significance, so far as I am aware, has never been commented upon.

Many of the beautifully complete skeletons of the small pterodactyls (Fig. 1), *Pterodactylus longirostris*, *P. brevirostris*, *P. elegans*, from the lithographic slate of Aichstädt, which were described many years ago by Goldfuss, Cuvier, Wagner and Soemmering, exhibit a marked opisthotonic curve to the neck and a more rigid appearance to the skeleton as a whole than is common among the skeletons of these remarkable vertebrates. *Pterodactylus*

<sup>1</sup> *Trans. Kansas Acad. Sci.*, 1890, p. 1.

*longirostris* Cuvier has the jaw gaping as if trismus was not an accompaniment of opisthotonos, such as is usually the case in recent times, or else the jaw was secondarily moved by the action of the water after the dissolution of



FIG. 1. *Pterodactylus micronyx* H. v. Meyer from the lithographic slates of Eichstätt in Bavaria. The original is in the paleontological collections at Munich. This specimen shows a typical opisthotonic position. One half natural size. After Broili.

the muscles. Other pterodactyls, such as *Pterodactylus scolopaceps*, *P. longicollum*, and others described by Plieninger<sup>2</sup> from the Jura of Swabia show no indication of any spastic distress.

The toothed bird (Fig. 2), *Archeopteryx macroura*, from the lithographic slates, commonly figured in the textbooks of geology, zoology, and paleontology, exhibits a pronounced opisthotonos, which may be slightly exaggerated in all the slender-necked vertebrates having a relatively heavy head. The weight of the head may have added to the curve, but the position is none the less a genuine opisthotonos. The skeleton of a small dinosaur,

<sup>2</sup> *Paleontographica*, Bd. LIII, pp. 210-313, 6 Tafeln, 1907.



FIG. 2. *Archaeopteryx macroura* from the lithographic slates, showing a typical opisthotonos.  $\times \frac{1}{4}$ .

about the size of the modern turkey, described and figured by Hoernes as *Compsognathus longipes* Wagn. (Fig. 3) from the lithographic slate of Kelheim, exhibits an unusually well-developed opisthotonos, the skull lying far back over the pelvis.

Probably the most complete representation of opisthotonos among fossil vertebrates is that seen in the skeleton of the small cursorial dinosaur, *Struthiomimus altus*

(Fig. 4) described by Osborn<sup>3</sup> from the Belly River series. The skeleton of this interesting dinosaur is mounted in a panel mount where the skeletal parts are placed approximately as found (Fig. 4). The attitude is typically opisthotonos, the jaws exhibiting trismus, with the head



FIG. 3. *Compsognathus longipes* Wagner, from the slates of Kelheim. The position of the head and tail are characteristic expressions of a tetanic spasm. After Hoernes.

thrown sharply back over the sacrum, the tail thrown sharply up; the toes strongly contracted, with the

<sup>3</sup> Osborn, H. F., 1917, "Skeletal Adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*," *Bull. of the Amer. Mus. Nat. Hist.*, Vol. 35, pp. 733-771, Pl. XXIV.

phalanges closely appressed. The whole attitude of the body strongly suggests some severe spastic distress. The animal may have been a plant feeder and its death and spastic distress due to feeding on some poisonous plant, such as to-day causes tetanic spasms in animals. It may have suffered death from a severe cerebrospinal infection, but whatever the cause of its death, the attitude of the



FIG. 4. Skeleton of *Struthiomimus altus*. Genotype specimen, Amer. Mus. 5339.  $\frac{1}{30}$  natural size. In this panel mount the animal is placed approximately as found. The attitude is typically opisthotonic. After Osborn.

animal strongly suggests the effect of disease, and in discussing the history of disease among animals the opisthotonic position exhibited by fossil skeletons must be considered as indicating a possible diseased condition.

The correlative phenomenon, pleurothotonos, is less common among the higher vertebrates, but is not uncommon among the fishes. This is evidently the attitude assumed by the skeleton of the plesiosaur, *Plesiosaurus macrocephalus* (Fig. 5), collected by Miss Mary Anning from the Lias of Lyme Regis, England, and figured by William Buckland in his "Bridgewater Treatise."<sup>4</sup> It is improbable that the head of this long-necked plesiosaur could have been turned into its present attitude by a current of water, since a force sufficiently strong to have moved the heavy head to one side would doubtless have

<sup>4</sup> Vol. II, Pl. 19, Fig. 1, 1837.



disturbed other portions of the body, and there is no evidence of this in the skeleton.

The remarkable specimen of *Geosaurus gracilis* H. von Meyer, from the upper Jurassic lithographic slate of Eichstätt, Bavaria, as described and illustrated by von Ammon, shows a clearly marked instance of pleurotho-

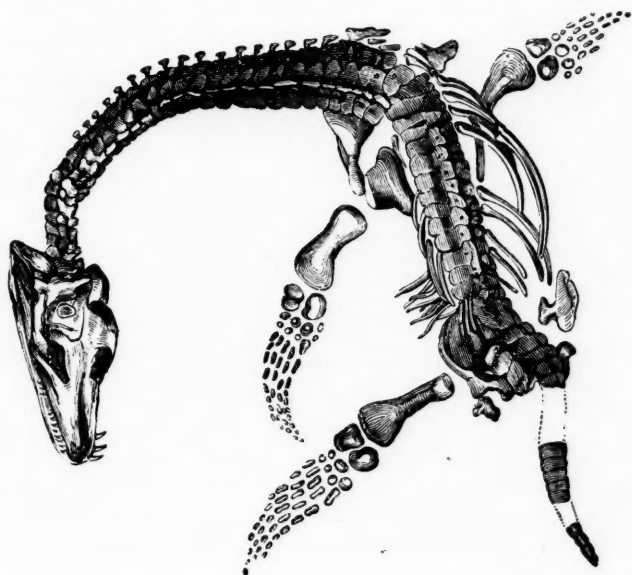


FIG. 5. *Plesiosaurus macrocephalus*, a skeleton from the Lias of England, preserved in a pleurothotonic attitude. After Buckland.

tonos. The body, slightly twisted, is bent into a strong, uniform arch toward the left, the animal having been preserved on its belly.

The fishes often assume at death and are fossilized in the pleurothotonic attitude. This is clearly indicated in the fishes from the Solenhofen, *Leptolepis sprattiformis*, as figured by Dreverman, Gaudry and others, though this attitude is also clearly that of fishes attempting to flop out of the soft mud back into the water. It is not a necessary sequence that all laterally compressed verte-

brates assume the pleurothotonic attitude, since often the ganoid fishes (Fig. 6), especially, assume the opisthotonos. It is true that the majority of fishes which are preserved in an approximately complete manner exhibit no trace of either of these attitudes. The great series of Triassic fishes from Connecticut seldom exhibit indica-



FIG. 6. *Acanthodes gracilis* F. Roemer, a ganoid fish from the Permian of Klein-Neundorf, Lower Silesia, showing an opisthotonic position. After Hoernes. Hoernes.

tions of either of these phenomena. A single specimen of *Catopterus gracilis*, of those figured by Eastman,<sup>5</sup> exhibits the opisthotonos, and a single one, *Ptycholepis marshi*, exhibits pleurothotonos. Of the scores of specimens of these fishes described by Newberry and Eastman a very small percentage show any sign of spastic distress.

As a clinical manifestation of great severity, opisthotonos and the correlative phenomena, pleurothotonos and emprosthotonos (episthotonos), have long been well known in human beings as accompanying certain phases of tetanus, abscesses of the brain, otitis media, hysteria, cerebrospinal meningitis, strychnine poisoning, and other afflictions, in which toxins affecting the nervous system are liberated. In these manifestations the muscles of the body, the spine and the extremities are strongly flexed. This characteristic attitude of the spasm has been graphically figured (Fig. 7) by Sir Charles Bell in his "Anatomy of the Expressions," where he says:

I have here given a sketch of the true Opisthotonos, where it is seen that all the muscles are rigidly contracted, the more powerful flexors

<sup>5</sup> Bulletin 18, State of Connecticut, State Geol. and Natl. Hist. Survey, Pl. IX.

prevailing over the extensors. Were the painter to represent every circumstance faithfully, the effect might be too painful, and something must be left to his taste and imagination.

Opisthotonos has also been described by Falls<sup>6</sup> as occurring in the fetus in utero, the cause for which is still unknown.

It is a matter of great interest to find these same manifestations represented in the fossilized skeletons of ancient vertebrates. The majority of the attitudes assumed by the fossils may be due to the spasm usually incident to death, the *Todeskampf* of the Germans, or to acci-



FIG. 7. Charles Bell's drawing of a man in opisthotonos.

dental shifting after death. Many of the vertebrates whose skeletons are found in anything like a complete state of preservation do not show these manifestations. It is on the whole unusual for fossil vertebrates to show opisthotonos and much more common in the slender-necked species. It is possible that the animals whose skeletons are preserved in the above-mentioned attitudes had suffered death owing to diseases similar to tetanus, cerebrospinal meningitis, or similar disturbances.

The skeleton of *Mesosaurus brasiliensis* from the

<sup>6</sup> Surgery, Gynecology and Obstetrics, January, 1917, pp. 65-67.

Permian of Brazil<sup>7</sup> exhibits a slight degree of opisthotonos (Fig. 8) such as is common in the death struggle of many modern vertebrates. There can be, I think, little doubt that many of the opisthotonic attitudes assumed by fossil vertebrates are easily explained as a phenomenon accompanying the "Todeskampf," but whether all can be so

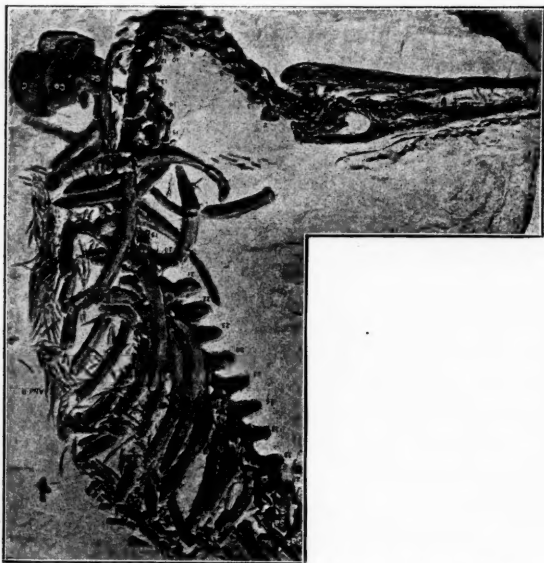


FIG. 8. *Mesosaurus brasiliensis* McGregor from the Permian of Brazil, showing a slight opisthotonos. After McGregor.

explained on this basis is extremely doubtful. It is certainly not true that all vertebrates exhibit indications of such spasms. While complete skeletal remains of fossil vertebrates are relatively rare, yet there is a sufficient number preserved which have been described to determine the relative frequency of these positions.

In the many complete skeletons of fossil reptiles from the Eocene of France described by L. Lortet<sup>8</sup> only four,

<sup>7</sup> McGregor, J. H., 1908, "Commissao de Estudos das Mines, etc.," Pl. IV.

<sup>8</sup> L. Lortet, 1892, "Les Reptiles du Bassin du Rhône," Archives du Museum d'Histoire Naturelle de Lyon, Tome V, pp. 3-139, Pl. I-XII.

*Alligatorium Meyeri* (Pl. X), two specimens of *Alligatorellus Beaumonti* (Pl. XI), and *Crocodileimus robustus* (Pl. IX), exhibit any degree of the opisthotonic attitude. Only one, *Pleurosaurus Goldfussi* (Pl. VII), exhibits the pleurothotonos. The majority of the remaining skeletons figured show no spastic distress whatever. So that while we may say that these two positions are common they are rather the unusual than the usual state of affairs.

On the other hand the dinosaurs *Struthiomimus altus* and *Compsognathus longipes*, many specimens of small pterodactyls and the fossil bird *Archeopteryx* exhibit such a marked opisthotonic attitude as to lead one to infer some cerebral-spinal or other intracranial infection which would have been easily possible in the poorly protected brain case of these early vertebrates. It requires but a glance at the nature of the brain case of the early vertebrates to see how poorly protected the cerebrospinal spaces were. Ingress of infecting bacteria may have been through any of the numerous nerve or vascular foramina, through the thin cancellous walls separating the brain case from the sphenoidal sinus, and through the anterior end of the brain case which was often protected only by a membranous covering, by cartilage, or by very thin bony plates.

The possible presence of the infecting bacteria has been so well established by the investigations of Walcott,<sup>9</sup> van Tieghem and Renault,<sup>10</sup> that little need be said here concerning them. Walcott has described and figured bacteria from fossilized Pre-cambrian algæ of central Montana, supposedly *Micrococcus*, the bacteria being arranged in groupings characteristic of the *Staphylococcus* isolated from a case of Pemphigus neonatorum by Falls,

<sup>9</sup> Walcott, C. D., 1915, "Discovery of Algonkian Bacteria," *Proc. Natl. Acad. Sci.*, Vol. 1, p. 258, Figs. 2 and 3; 1914, "Pre-Cambrian Algonkian Algal Flora," *Smith. Misc. Coll.*, Vol. 64, No. 2 (Publication 2271).

<sup>10</sup> Renault, B., 1900, "Microorganismes des combustibles fossiles," *Bulletin de la Société de l'Industrie minière Saint-Etienne, Serie III*, 1899, Tome 13, pp. 865-1161; 14 (1-2), pp. 5-159, 1900, with Atlas, 1898-1899, Pl. X-XXV, Atlas, 1900-01, Pl. I-V.

by whose courtesy a photograph has been used for comparison. Renault has described a great variety of bacteria, many of which are apparently similar to the bacteria of to-day.

In searching for evidences of disease among fossil vertebrates I have been interested in making the above comparisons. In the light of the above study it seems probable that some of the instances of opisthotonos and pleurothotonos among fossil vertebrates may be due to acute cerebrospinal infections, the petrified skeletons exhibiting trismus, rigidity of the limbs, and the peculiar backward curvature of the vertebral column so common to-day as clinical manifestations of spastic distress. This is especially probable in the cases where the skeletons exhibit such marked opisthotonos and pleurothotonos as do many of the specimens above referred to. It may then be said that opisthotonos as seen in the skeletons of fossil vertebrates indicates disease only in those exaggerated cases of spastic distress as is evidenced by the attitudes assumed by fossil vertebrates, such as the small dinosaur, *Struthiomimus altus*, and the bird, *Archæopteryx macroura*. Not all vertebrates preserved in opisthotonus were victims of disease, but many of them suggest a strong neuro-toxic condition.

## CANCER'S PLACE IN GENERAL BIOLOGY

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THE condition which has been called cancer by the laity and the medical profession has been studied by the latter largely from the standpoint of disease. Investigators have considered its great destructive action, cause, prevention and treatment, all of which study has been stimulated by the urgent necessity of its eradication from the ills of man, and not in its relation to the known biologic facts concerning the universal conflict between living normal cells and their natural enemies. In order to approach correctly this biologic phase of the condition it will be necessary to answer the question: What is cancer?

To the pathologist, cancer is a cellular overgrowth which occurs in some multicellular organism, especially in man, and which is characterized by its apparently unlimited proliferation, during which it destroys tissues, and is fatal eventually to the whole organism. This, in general, is the conception held by the members of the medical profession, but to the scientific mind which is interested in and trained in the fundamental or more specific factors operating in living nature, it is neither satisfactory nor sufficient.

An analysis of the condition from such a biologic point of view necessitates also for its elucidation a study of the facts relative to the evolution of multicellular organisms from single cells as units of life. Biologists agree that the cell is the visible unit of life, and that all cells have certain fundamental structural and functional characteristics which are common to all. They further agree that all multicellular beings evolve by a process of division or segmentation of a single cell which has been stimulated automatically, or by the process of extrinsic fertilization to such activity.

During the process of segmentation certain dominant facts present themselves. A fertilized ovum, for exam-

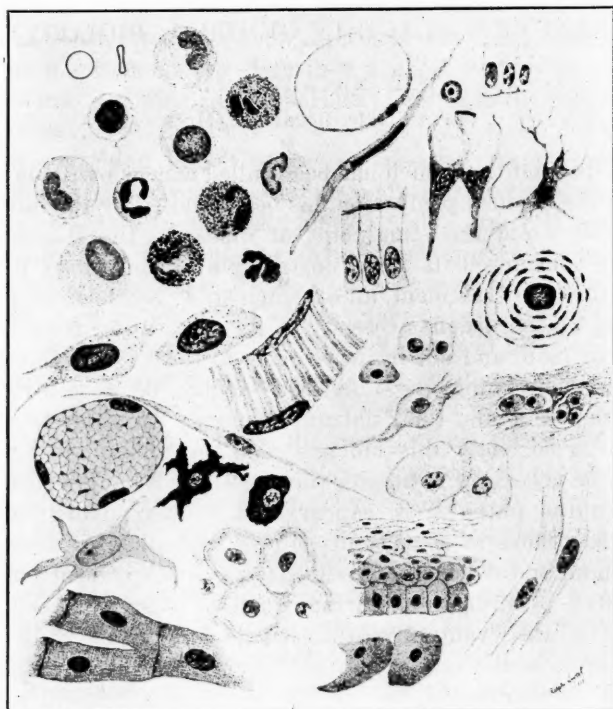


FIG. 1. Some of the differentiated cells (textocytes) of the human body:

*Biologic Terminology*

1. Erythrocytes,
2. Lymphocytes (small),
3. Lymphocytes (large),
4. Transitional forms,
5. Leukocytes,
6. Eosinocytes,
7. Mastocytes,
8. Fibrocytes,
9. Rhabdomyocytes,
10. Melanocytes,
11. Myxocytes,
12. Cardiomyocytes,
13. Lipocytes,
14. Leiomyocytes,
- 15, 18, 19. Adenocytes,
- 16, 24. Neurocytes,
17. Osteocytes,
20. Endothelocytes,
21. Chondrocytes,
22. Epithelocytes,
23. Tendocytes,
25. Sudorocytes,
26. Sebocytes,
27. Gustocytes.

*Medical Terminology*

- Red blood corpuscles.  
 Lymphocytes (small).  
 Lymphocytes (large).  
 Transitional forms.  
 Polymorphonuclear leukocytes.  
 Eosinophiles.  
 Mast cells.  
 Fibrous connective tissue cells.  
 Striated muscle cells.  
 Pigmented cells.  
 Muscle cells.  
 Heart muscle cells.  
 Fat cells.  
 Smooth muscle cells.  
 Glandular epithelium.  
 Nerve cells (neurones).  
 Bone cells.  
 Endothelial cells.  
 Cartilage cells.  
 Epithelial cells.  
 Tendon cells.  
 Sweat cells.  
 Sebaceous cells.  
 Taste cells (of a taste bud).



ple, divides; the cellular divisions divide; these continue to divide and form eventually, in a definite period, the millions of cells which constitute the organism. This is a simple statement of general facts, but coincidentally with these facts there is an orderly sequence of cellular changes which seems to be foreordained in the original fertilized ovum; the cellular progeny does not retain, to the same degree, all of the structural and functional characteristics of the original cell (ovocyte). There is a grouping of cells which is coincident with morphological

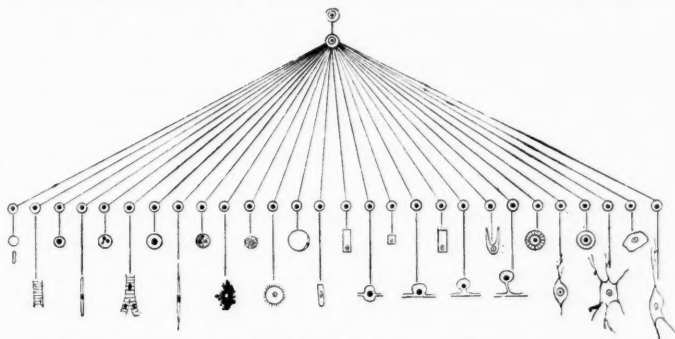


FIG. 2. In the embryonic evolution of adult tissues there are certain arbitrary stages of differentiation in which the cells may be given certain names.

During segmentation of the fertilized ovum (ovocyte) the daughter cells do not show any special morphologic characteristics of adult tissues, but are nevertheless forebearers of such tissues and may be called *prototoblasts*.

The textocytes, or tissue cells, are represented in this diagram by symbols derived from the characteristic outlines of the cells of specific tissues (Fig. 1).

After the prototoblasts align themselves into the positions of subsequent tissues they become the immediate forebearers of the tissues and may be called textoblasts. These cells develop by differentiation and specialization into the tissues (textocytes) of embryonic and adult life. Some of the cells remain undifferentiated (textoblasts) in adult life to form the reserve or regenerative cells for specific tissues when the latter are destroyed.

and functional differences. Out of such differentiation and specialization of cells, types of cells arise, groups of which constitute what are called tissues (adenotex, chondrotex, endotheliotex, epitheliotex, erythrotex, fibrotex, etc.) (Fig. 1). Two or more of the different tissues become grouped to form organs (tongue, esophagus, stomach, liver, kidneys, skin, etc.) which likewise are grouped to build up structural and functional systems (respiratory, alimentary, nervous, osseous, etc.), the combined qualities of which form the complete multicellular organ-

ism or being. Such orderly evolutionary facts apply to the development of all animal and vegetable multicellular beings (Fig. 2).

Out of the essential living properties of a single cell other cells develop which have in them an exaggeration of some essential initial quality, each tissue representing an exaggeration of some one quality. Such evolutionary cytologic organization produces a communism of living units, the combined apparent and dominant purpose of which is to live and reproduce its kind.

A biologist, if asked the ultimate purpose of life, would shake his head and say he did not know, but asked the immediate and dominant purpose, would say the protection of life and this protection even at the expense of life, an apparent contradiction which has been recognized but not comprehended even by scientists. The evidence of this great protective purpose of living matter is too universal to be called to the attention of the least observing; it works automatically and in a large degree independently of the will of living beings.

This fundamental vital protective purpose forms the basis of the following consideration of cancer's place in general biology: It presupposes, and observation substantiates it, that all living cells have natural antagonists against which protection is necessary; and that there is a conflict in nature during which there is constant building up and tearing down of things living. The human body is no exception to this rule, as every physician and layman knows. The tearing down is called disease, and the rebuilding is called regeneration, repair and healing.

The partial destruction of a human tissue by animate or inanimate antagonists may be followed by its regeneration; the complete destruction may be followed by repair or replacement, but not by its regeneration.<sup>1</sup> The

<sup>1</sup> This statement may not seem to be true when applied to some of the lower forms of life such as the earthworm (*Allolobophora fatida*) and the planaria, in which organizations certain tissues are regenerated after apparent complete destruction. The destruction is, however, not complete in such cases, because the normal regenerative power resides in other cells, which by the process of metaplasia build up tissues they do not form in the normal sequence of evolution.

degree of regeneration of tissues, according to the observations of biologists, is in an inverse ratio to the degree of their specialization and differentiation. One finds, therefore, this regenerative factor a variable and unequal quantity among tissues of the human body. The protective tissue cells (epitheliocytes) of the skin, for example, are readily regenerated if not completely destroyed over a large area; the cells of the retina, in all probability, are never regenerated even after partial destruction. Fibrocytic, erythrocytic, epitheliocytic and leucocytic tissues, in all probability, represent types, the special functions of which show the highest degrees of regeneration.

In many tissues of the body, coincidentally to normal communistic activity, there is constant or periodic normal destruction with constant or periodic regeneration, both of which depend on communistic functional activity and a constant or periodic destructive action of antagonistic agents. The amount of regeneration depends on the amount of destruction, which depends on the quality, quantity and duration of action of the destructive agent or agents.

Tissue destruction and regeneration were made the subject of investigation by the writer, in the protective cells of the human skin (Fig. 3) and in the secretory epithelium of the human mammary gland (Fig. 4). One finds in these organs that some unknown irritant or irritants of an apparent low degree of virulence, acting over a prolonged period of time, produce certain reactive cellular phenomena; there is first a destruction of the specialized and differentiated cells (textocytes). This destruction is associated with an hypertrophy of the so-called basal cells (cells of the stratum germinativum, or textoblasts) and a lymphocytic infiltration in the supporting stroma.

Space does not permit a consideration of the factor of lymphocytic infiltration. The hypertrophy of the so-called basal cells, however, is of great importance from the standpoint of the subject under consideration.

One sees clearly that nature, in building up the special-

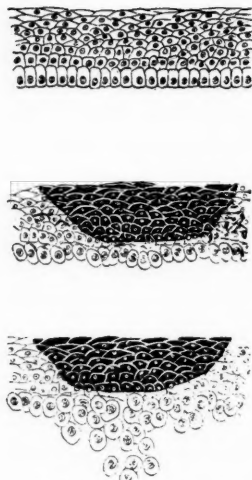


FIG. 3. Three diagrammatic histologic stages of reaction of textoblasts of the epithellum of the skin under normal and certain destructive conditions. (a) Normal epithellum showing the relative position of textocytes and textoblasts. (b) Destruction of the textocytes is indicated by the shaded portion. The response to chronic destruction is an hypertrophy or an hyperplasia of the textoblasts. This hyperplasia takes place with and without differentiation into textocytes, depending on the degree and chronicity of the destruction. In this condition it is impossible to state from the morphologic appearance whether the cells will become differentiated or remain undifferentiated. (c) Represents the stage of migration of the hyperplastic undifferentiated textoblasts.

they retain their oval or spheroidal form, become larger and produce a massed overgrowth of undifferentiated cells (Figs. 3 and 4). The degree of hyperplasia and migration varies under different and perhaps the same irritative circumstances, depending on inherited variable

ized and differentiated protective cells of the skin and the secretory cells of the mammary gland, has also made provision for an anticipated destruction, an anticipation which is no more remarkable in nature than that of the butterfly which deposits its eggs in a safe place and dies with the inherent assuredness that the eggs will some day develop into caterpillars and eventually into butterflies to continue the existence of the kind. In the case of the cells of the skin and the mammary gland, if the irritant is removed, complete regeneration of differentiated or specialized cells takes place, provided the basal cells themselves have not been completely destroyed.

Continuance of the action of the destructive agent or agents produces hypertrophy, hyperplasia and migration of the basal or regenerative cells (Figs 3 and 4). Coincidentally with such a hyperplasia the basal cells (textoblasts) do not always become differentiated to the form of the specialized squamous or secretory cells according to their communistic normal foreordination;

factors in the basal cells the neighboring tissue cells, their food supply, natural drainage, and perhaps some unknown factors. The significant biologic facts rest

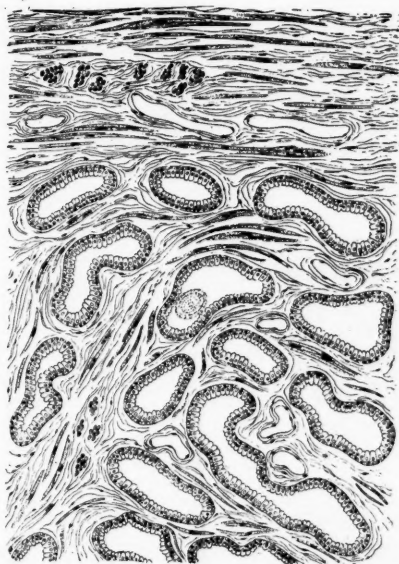


FIG. 4. Diagrammatic relation of the glandular units to the other tissues.

in the attempted cellular regeneration by hypertrophy and hyperplasia and the effort to change environment by migration, all of which may be seen not only in the breast and skin, but also in the specific cells of the hair follicle, prostatic gland and stomach (Figs. 5, 6 and 7).

A change of environment through overgrowth or migration often stimulates or allows an attempt at differentiation into the specific tissue-cells for which the original reserve or regenerative cells (textoblasts) were apparently foreordained in the normal evolution of tissues. This is evident in cancerous new growths which have migrated into other tissues, and in regional lymphatic glands, which are the favorite locations of environmental change for such migrants.

Cellular regenerative reaction takes place in one or both of two ways; there is hyperplasia with or without

differentiation. An hyperplasia with differentiation into specific tissue-cells may be called *texto-typic* in contradistinction to that without differentiation, which may be

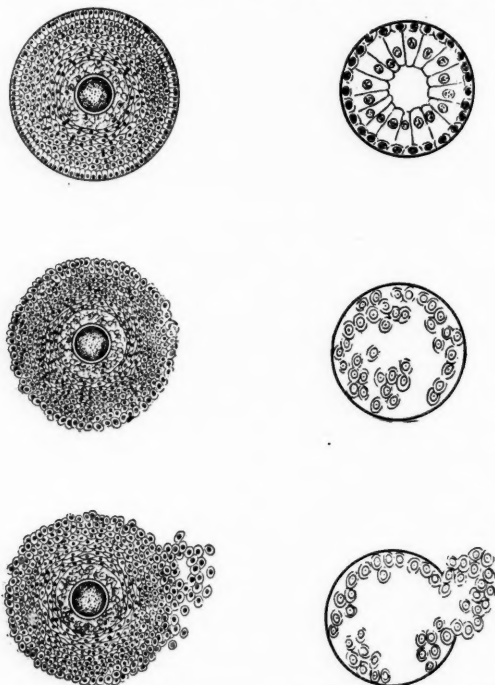


FIG. 5. The reaction to destruction of textocytes in the hair follicle. A. Primary pilo-cytoplasia. B. Secondary pilo-cytoplasia. C. Tertiary pilo-cytoplasia.

FIG. 6. The reaction to destruction of textocytes in the prostatic acinus. A. Primary adeno-cytoplasia. B. Secondary adeno-cytoplasia. C. Tertiary adeno-cytoplasia.

termed *cytotypic*. This occurs before and after migration.

According to writers on the subject of cancer the principal criterion for the denotation of a condition by this term consists of the destructive migration of tissue-cells. Such neoplasms have been often considered to be direct derivatives of tissue-cells, because their cells sometimes resemble those of specific tissues of organs from which they have arisen. As a matter of fact the malignant neoplastic cells (*neocytes*) do sometimes resemble the



Primary Cytoplasia

Secondary Cytoplasia

Tertiary Cytoplasia

FIG. 7. The reaction to destruction of textocytes in the gastric tubules. A. Primary adeno-cytoplasia. B. Secondary adeno-cytoplasia. C. Tertiary adeno-cytoplasia.

specific tissue-cells of the site of origin, but this is not evidence that the tissue cells themselves have been converted into the cells, which at best never are morphologically and functionally identical with the original tissue-cells.

According to the observations of the writer, the cells which constitute cancer are the progeny of the partially differentiated or reserve cells (textoblasts) which have for their natural communistic function the protective restoration of the specific tissues when the latter have been destroyed. It may be asked, how can a condition which will certainly destroy the whole organism be the result of a protective principle? This perfectly natural question can only be answered by stating a general principle in biology, namely, that regenerative changes do not always consider the communistic adaptation of the whole organism. It is a manifestation of a principle which is inherent in cells, cytologic life being primary, and tissue or organic life secondary. Thus, the planarian in response to certain stimuli produces a new head when it already possesses one; the actinian produces a new mouth on the side of its body under certain regenerative conditions. Protective migration of animals as a result of food famine leads to their complete destruction not infrequently.

In the case of the human being there is no more fitting example of a fatal, protective communistic action of cells than that which occurs when a human being obtains a severe and destructive burn about the mouth or in the esophagus. Under such circumstances the fibroblasts in the region become hypertrophic, hyperplastic, differentiated and specialized into dense, contracting scar-tissue, which, if the destruction has been great enough, may, as a communistic, regenerative, protective process, inherent in the fibroblasts, completely close the orifice of the mouth or esophagus, the result of which is starvation and destruction of the whole organism. The fibroblast's evolutionary duty in the communism is that of replacing losses of other tissues, and the duty is performed in this incidence at the expense of its own life and the life of the organism. Thus, it may be seen that communistic life is secondary to the life of the cells even in such a wonderful and complex organization as the human body.

The hyperplasia or neoplasia does not even have to be migratory from a cellular standpoint to destroy the whole organism and thereby be clinically malignant; a term which has been utilized by the medical profession largely to differentiate cancer from other neoplastic conditions which are generally conceived of as benign. Thus, a fibroid tumor of the uterus may be clinically malignant and still not show cytologic signs of the malignancy so characteristic of cancer.

Biologically speaking, protection may be divided into types—cytotypic, textotypic, organotypic, systemotypic, organismotypic, familiotypic, raciotypic and speciotypic, etc. Cancer represents the cytotypic protection which is of primary importance in all protection of living protoplasm.

From a biological standpoint the three reactions of regenerative cells of tissues to antagonistic influences are hypertrophy and hyperplasia with differentiation, hyperplasia without differentiation, and hyperplasia with migration, with or without partial differentiation. These three conditions have been termed cytoplasias (condi-





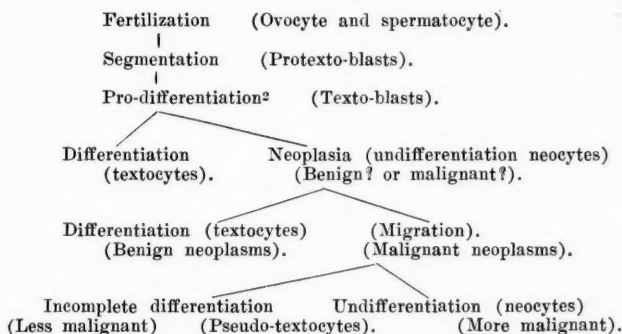
Such a nomenclature of known reactive facts has served the writer as a convenient, simple and practical, biologic, histologic and clinical terminology. The writer does not mean that these terms should be utilized to designate neoplasms. They apply only to the tissue-reaction, which is, after all, the essential thing to be considered. Animal and vegetable neoplasms represent only phases of such reaction.

From a clinical standpoint, a hypertrophy and hyperplasia with complete tissue differentiation (restaurocytoplasia) represents tissue regeneration, which is a benign condition, since it is normally reconstructive from a communistic standpoint instead of destructive. A hyperplasia without tissue differentiation (expandocytoplasia) represents a condition of the cells in which no one can foretell whether the cells will become differentiated into tissues, and thereby be constructive, or migrate and become destructive.

Such a condition is, therefore, in the presence of science, a questionable condition. Its benignancy or malignancy, in so far as the organization is concerned, with our present knowledge, can not be forecast. The probability of possible migration may be suspected from the frequent morphologic identity of these undifferentiated cells to the migratory cells of a known malignant or cancerous condition, the only difference being their location.

Biologically considered, primary cytoplasia represents a tissue regenerative condition, the secondary cytoplasia represents a neoplastic condition, and tertiary cytoplasia represents a neoplastic migration to regions foreign to the cells in question. The whole field of tissue replacement, tissue regeneration and benign and malignant (cancerous) neoplasmata (new growths) is comprehended in these three groups.

The following diagram represents the relation of malignant (cancerous) and so-called benign neoplasms to the evolution and organization of the human body:



Briefly, in conclusion, the writer makes the following generalizations from his experience in his studies of cancer's place in general biology:

1. All multicellular organisms represent communisms of cells which have divided their labors and become specialized and differentiated to form tissues.

2. Nature has provided for the regeneration of most, if not all, tissues when the tissues are partially destroyed by antagonistic forces.

3. In many animal and vegetable tissues the regenerative cells respond to tissue-destruction in three degrees, *i. e.*, hypertrophy, hyperplasia and migration.

4. During hyperplasia with or without migration the cells sometimes attempt to differentiate.

5. Limited hyperplasia with complete differentiation produces tissue replacement. Unlimited hyperplasia without complete differentiation produces the so-called malignant neoplasms.

6. Cancer represents an unlimited hyperplasia of regenerative cells of tissues plus migration without complete differentiation.

7. Regeneration (hyperplasia) without differentiation is a cytotypic protective process.

8. Regeneration (hyperplasia) with differentiation is a textotypic protective process.

9. Cancer is a cytotypic instead of a textotypic protective process.

10. In nature cytotypic protective processes are sometimes fatal to the communism of which the reactive cells are a part.

11. All of the reactions may be designated by a simple biologic terminology which standardizes clinical, histologic and biologic facts.

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<sup>2</sup> The stage of pro-differentiation exists prenatally and postnatally and may be distinguished terminologically by calling the prenatal cells of segmentation prototoblasts and the regenerative postnatal cells textoblasts.

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## A SURVEY OF THE HAWAIIAN CORAL REEFS

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DURING a residence of nearly ten years in the Hawaiian Archipelago the writer has had opportunity of visiting and exploring many of the coral reefs, and has been much interested in their formation, flora, and fauna. The present paper aims to present the salient and significant facts relating to the natural history of these remarkable reefs, in compact and largely non-technical form. There is a large scattered literature (inaccessible to the average reader), dealing with the coral reefs and their life, but the writer believes this to be the first time that the following data have appeared within the confines of a single paper.

The Hawaiian Archipelago is situated in the midst of the North Pacific Ocean. It lies between latitudes  $18^{\circ} 54'$  and  $22^{\circ} 14'$  and  $154^{\circ} 48'$  and  $160^{\circ} 13'$  West Longitude, being about 2,020 miles southwest of San Francisco. Its east and west extension is nearly two thousand miles. The islands are but the apices of a titanic mountain range that rises to heights of from three to five miles from the floor of the ocean.

This long archipelago, comprising about twenty-two islands, is remarkable for the simplicity of its geologic formations. Only two classes of rock material are known in the entire group—lava and coral. There are numerous subdivisions of these groups (for example, there are many varieties of lava), but all the known rock-formations give conclusive evidence of having originated from either one of two sources—volcanic or coralline. It is extremely interesting to consider that all of these islands are compounded of two such diverse elements—one from a roaring lake of incandescent lava; the other from the age-long

labors of coral polyps. A strange "partnership," without parallel in the annals of natural history.

The islands of the Hawaiian group may be classified on this basis. The large, high islands of the eastern portion of the archipelago are composed almost wholly of lava, with small fringing reefs. The low, small islets that comprise the western extension of the archipelago are made almost wholly of coral, that is, in so far as their exposed portions are concerned. The coral formations undoubtedly rest upon a volcanic substratum. The grouping may be expressed as follows:

- I. Large mountainous lava islands, forming a compact group at eastern end of archipelago; elevations over 1,000 ft.
  - A. With well-developed fringing reef:  
Niihau, 1,300 ft.; Kauai, 5,250 ft.  
Oahu, 4,040 ft.  
Molokai, 4,958 ft.; Lanai, 3,400 ft.; Kahoolawe, 1,472 ft.
  - B. With scanty fringing reef:  
Hawaii, 13,825 ft.; Maui, 10,032 ft.
- II. Small, low islets, scattered along the western axis of the archipelago; elevations below 1,000 ft.
  - C. Eroded volcanic blocks, 120-900 ft., with fringing coral reef: Nihoa, French Frigates Shoals, Gardner I.
  - D. Elevated coral islands, 45-55 ft., with fringing reef: Laysan, Lisianski.
  - E. Typical coral atolls: Pearl-and-Hermes, Midway, Ocean.
  - D. Reefs with visible surf, but no exposed coral: Maro Reef, Dowsett's Reef.

The entire series, named in sequence from east to west, is: Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, Niihau, Nihoa, Necker, French Frigates Shoal, Gardner, Dowsett's Reef, Maro Reef, Laysan, Lisianski, Pearl-and-Hermes, Midway, Ocean. The two extremes—Hawaii and Ocean Island—present a contrast of wonder-

ful vividness. Mauna Loa, the greatest active volcano on the planet, dominates the island of Hawaii. Its colossal dome is crowned by a summit lake of reverberating liquid lava, with spectacular displays of high-jetting fire fountains. The bulk of the island is still growing, through intermittent outpourings of lava. Ocean Island, on the other hand, is the last white fragment of a subsiding coral-crowned mountain—perhaps a dead volcano, that may have resembled Loa in many respects, but which has been drawn inexorably into the abysses of the Pacific. One represents the culmination of the volcanic forces; the other the climax of coral work—an atoll on a tropic sea.

Of the larger eastward islands, Kauai and Oahu are of particular interest, as they have the largest coral reefs, and support the most luxuriant marine life. The reefs are all of the fringing or platform type, and vary in width from a few hundred feet to half a mile. Reefs are well developed along the southern or leeward shores of the two islands mentioned, and also, to a lesser degree, along the northern coasts. Oahu is almost encircled by coral reefs, whereas Kauai, Molokai, and Maui have numerous coastal stretches wholly free from coral. The little island of Niihau, to the west of Kauai, has considerable coral reef.

It is significant to note that although the majority of corals, particularly the more massive reef-building forms, occur only in the shallow waters of tropic seas, there are a number of species that inhabit deep, cold waters. *Lophohelia prolifera* and *Dendrophyllia ramea*, for example, form dense beds at depths of from 600 to 1,200 ft. off the coasts of Norway, Scotland, and Portugal. The general requirement, however, is shallow water whose mean temperature does not fall below 68° F., and the reef-building species do not flourish unless the temperature is considerably higher. Although a single Hawaiian species of mushroom-like coral (*Bathyactes hawaiiensis*) was dredged by the *Albatross* from a depth of nearly 7,000 ft., most of the Hawaiian forms live in waters of

6-150 ft. depth. Of the 34 Hawaiian genera, 14 habituate this shallow-water zone throughout the archipelago, and 10 of these occur on the leeward reefs of Oahu between Leahi and Pearl Harbor.

Dana's<sup>1</sup> comprehensive statement concerning the reef-building corals may be compactly summarized. He states that it is important to have a correct apprehension of what are those reef species as distinct from those of colder and deeper seas. The coral-reef species of corals are the following:

1. In the *Astræa* tribe, all the many known species.
  2. In the *Fungia* tribe, almost all the known species.
  3. In the *Oculina* tribe, all of the *Orbicellids*; part of the *Oculinids* and *Stylasterids*; some of the *Caryophyllids*, *Astrangids*, and *Stylophorids*; all of the *Pocilloporids*.
  4. In the *Madrepora* tribe, all of the *Madreporids* and *Poritids*; many of the *Dendrophyllia* family.
  5. Among *Alcyonoids*, numerous species of the *Alcyonium* and *Gorgonia* tribes and some of the *Pennatulacea*.
  6. Among *Hydroids*, the *Millepores* and *Heliopores*.
  7. Among Algæ, many *Nullipores* and *Corallines*.
- He further states that

Through the *torrid* region, in the central and western Pacific, that is, within 15° to 18° of the equator, where the temperature of the surface is never below 74° F. for any month of the year, all the prominent genera of reef-forming species are abundantly represented. The Hawaiian Islands . . . are outside of the torrid zone of oceanic temperature, in the *subtorrid*, and the corals are consequently less luxuriant and much fewer in species. There are no *Madrepores*, and but few of the *Astræa* and *Fungia* tribes; while there is a profusion of the corals of the hardier genera, *Porites* and *Pocilliporæ*.

The more abundant reef builders, at moderate depths, are the madrepores, astræids, porites and meandrinæ. At depths of 90-120 ft. the millepores and seriatopores predominate. The great field of coral development thus lies between low water and 120 ft.

Dana's classification of reef-formations is useful in surveying the Hawaiian reefs:

<sup>1</sup> James D. Dana, "Corals and Coral Islands," 1872.



1. *Outer reefs*, or reefs formed from the growth of corals exposed to the open seas. Of this character are all proper barrier reefs, and such fringing reefs as are unprotected by a barrier. All of the larger Hawaiian reefs are of this character.

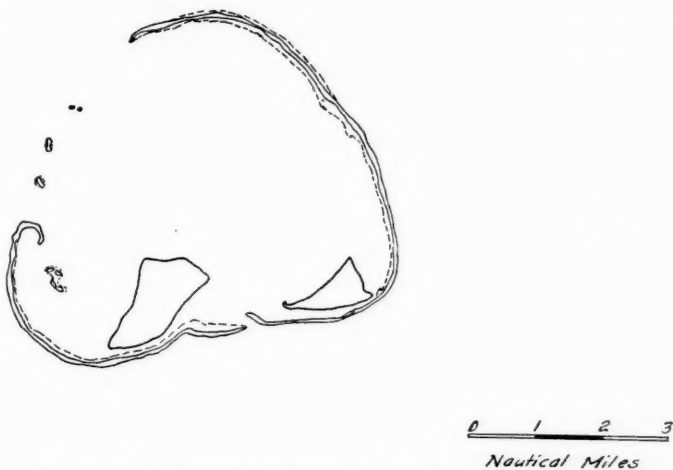


FIG. 1. Midway Island. A nearly complete circular coral atoll, about 16 miles in circumference; area of lagoon about 38 sq. miles; several low sand islets in the lagoon.

2. *Inner reefs*, or reefs formed in quiet waters between a barrier and the shores of an island. The reefs of this type are very rare in Hawaii; usually they are mere hummocks in the lagoon of the fringing reef.

Kaneohe Bay and Pearl Harbor, on Oahu, are essentially large drowned valley regions, converted by subsidence into land-locked bays, which have become more or less completely barred and filled by coral growths. Were there not such large quantities of fresh, mud-laden water poured into these bays, they would be veritable coral wonderlands, for it is in protected waters of inner channels or lagoons that corals attain their finest development, and the "richest views are presented to the explorer of coral scenery."

The marine flora and fauna in these bays presents

many contrasts with those of the true lagoons and outer reef rims. All of the pure-sea-water-requiring organisms are wholly absent or rare, and in their places one finds a large series of brackish water and silt-loving forms. The generalization is quite accurate for the Kaneohe and Pearl Harbor inner reefs that

The main distinction between the inner and outer reefs consists in the less fragmentary character of the rocks in the former case, the less frequent accumulations of débris on their upper surface, and the more varied features and slopes of the margins. . . . There is to be found about inner reefs, over large areas, solid white limestone, showing internally no evidence of its coral origin, and containing rarely a shell or other imbedded fossil. It is a result of the consolidation of the fine coral sand or mud that is made and accumulated through the action of the light waves that work over the inner reefs. Other portions of reef consist of branching corals, with the intervals filled in by sand and small fragments; for even in the stiller waters fragments are to some extent produced. A rock of this kind is often used for buildings and walls on the island of Oahu. It consists mainly of *Porites*, and in many parts is still cavernous, or but imperfectly cemented.<sup>2</sup>

3. *Channels or seas* within barriers, which may receive detritus either from the reefs, or from the shores, or from both these sources combined. These channels correspond to the lagoons of the fringing reef, except that the channels are much larger. The Hawaiian lagoons are generally floored with coral sand, indicating that reef erosion is more rapid than coast erosion.

4. *Beaches and beach formations*, produced by coral accumulations on the shore through the action of the sea and winds. Beaches and dunes of coral sand are common on the islands of Molokai, Oahu, Kauai, Laysan, Midway, Ocean, etc.

Of the three great classes of coral reefs—fringing, barrier, and atoll—the first and last only have representation in the Hawaiian Archipelago. The fringing reefs are platforms of coral limestone which extend but a relatively short distance from the shore. The seaward edge of the platform is characteristically somewhat higher than the inner portion, and is usually awash at low tide. The reef

<sup>2</sup> Dana, *loc. cit.*

is cut by more or less numerous channels, which mark those places where streams flow down from the land. There is usually a lagoon—of sufficient depth to be navigable by canoes or small boats—between the reef rim and the shore. The outer wall of the fringing reef is steep, and in the Hawaiian Islands descends abruptly into deep water. The reef rim is the region of most active coral growth, the shoreward coral being gradually killed by fresh water and the deposition of mud and sand.

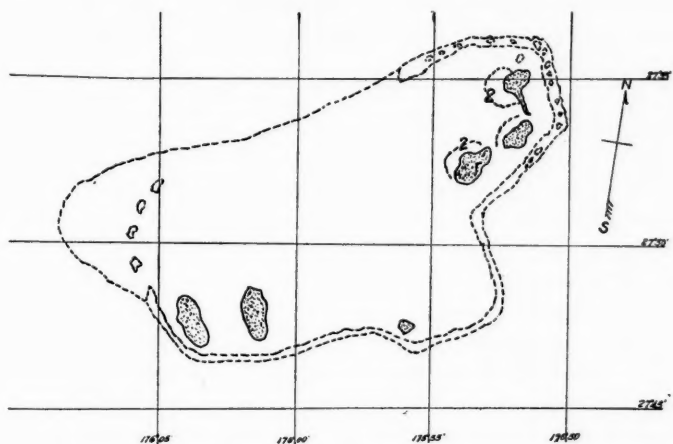


FIG. 2. Pearl and Hermes Reef. An irregular, oval coral atoll, 42 miles in circumference; area of lagoon about 80 sq. miles; numerous low sand islets in the lagoon. The soundings (2) are in fathoms.

Barrier reefs may be considered as fringing reefs upon a large scale. Although rare in the North Pacific Ocean, there are many fine examples in the South Pacific. The grandest in the world is the Great Australian barrier reef, which is 1,250 miles long, and supports a wonderfully rich marine life.

An atoll is an annular or ring-shaped reef, either awash at low tide or surmounted by several islets, or less frequently by a complete circle of dry land surrounding a central lagoon. The outer wall of the atoll generally descends with a very steep but irregular slope to a depth of

3,000 ft. or more. The central lagoon is seldom more than 60 ft. deep, and is often much less. There are usually one or more navigable passages leading from the lagoon to the open sea.

The thickness of the Hawaiian reefs is an engaging subject for speculation. Many of the reefs are undoubtedly several thousand feet thick at their seaward margins. Dana writes:

Could we raise one of these coral-bound islands from the waves, we should find that the reefs stand upon submarine slopes, like massy structures of artificial masonry; some forming a broad flat platform or shelf ranging around the land, and others encircling it like vast ramparts, perhaps a hundred miles or more in circuit.

The late Dr. S. E. Bishop, of Honolulu, estimated the depth of the coral at Barber's Point, Oahu, to be 2,500 ft.

Our first exploration of a Hawaiian coral reef, some ten years ago, made a lasting impression, so novel and vivid were those initiatory experiences. The tropic morning was fine and clear, with the clouds heaped along the mountains, and the seaward sky flawless. The trade winds were unusually quiet and the tide was at lowest ebb. All conditions were most favorable for a detailed examination of the reef. My comrade and I embarked in a native outrigger canoe and paddled from the well-known Waikiki Beach, near Honolulu, to the white surf-lines of the reef-rim. This is one of the richest portions of the Oahu fringing reef, from the biological standpoint. We were clad in bathing suits and provided with suitable collecting apparatus and water-boxes—glass-bottomed boxes by means of which the sunlit translucent waters are easily surveyed.

Arriving at a suitable location, a thousand feet from the shore, where the water was scarcely two feet deep, we anchored the canoe and prepared for wading. We were equipped with old shoes to protect our feet from the coral (which can cause very painful and slow-healing wounds); with broad-rimmed hats to protect eyes, face, and neck from the intense glare of sun and water; with hammers

for breaking up the coral blocks and for loosening material; and with sundry haversacks, wide-mouth bottles, formalin, etc. For three entrancing hours we wandered over the ledges, knolls, and sandy pockets of the reef, bewildered by the luxuriant diversity of marine life. Fantastic clumps of living coral, a large number of strange molluscan species; bright-spotted crabs and other

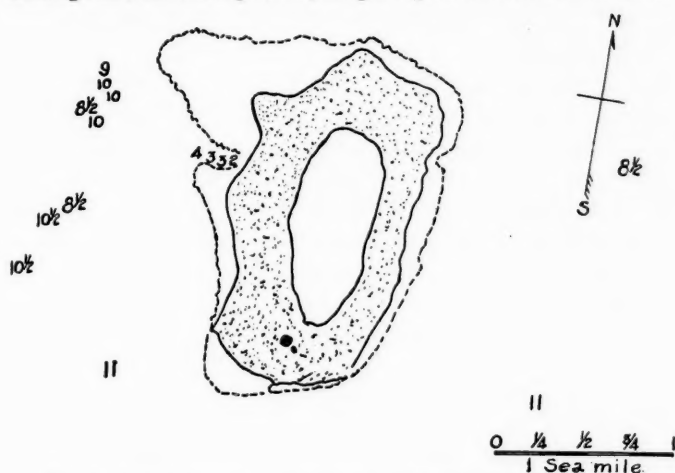


FIG. 3. Laysan Island. An elevated coral island, with a central lagoon. The soundings are in fathoms, as in all the maps. The dotted line indicates the reef rim; this also applies to all the maps.

crustaceans in an array of shapes and sizes; colonies of sea-urchins; spidery-armed brittle-stars; exquisitely beautiful hydroid colonies; bizarre-hued holothurians; and everywhere marine algae of many tints and shapes, representing a long list of interesting genera. Gorgeously colored fishes, small and large, lurked in the shadowy reef pools, and evaded prolonged inspection. It is impossible to describe the profound impression produced by one's first sight of the strange and fascinating reef-world.

The coral fauna of the Hawaiian reefs, although not as rich nor as diversified as those of more tropical waters, is not to be regarded as scanty. Dr. T. Wayland Vaughan, who thoroughly investigated the *Albatross* and Bishop

Museum collections, reports 15 families, 34 genera, and 123 species, varieties and forms. As Bryan<sup>3</sup> states,

Some idea of the richness of the coral fauna of any given locality can be gathered from the fact that the reef and shallow waters along the south side of Oahu, but especially at Waikiki, yielded examples of thirty-four of the species enumerated.

Of the Hawaiian stony corals (Madreporarians) the genus *Porites* is the most abundant and is represented by the largest number of species and varieties. *Pocillopora* ranks next in importance, followed by *Montipora*, *Pavonia*, *Favia*, *Leptastrea*, *Cyphastrea*, and *Fungia*. The last-named genus merits special mention because of the unique shape of the skeleton, which closely resembles the inverted head of a fully expanded mushroom, hence the name mushroom coral. These are solitary, and fairly common. They are usually found lying flat on the floor of little pools or pockets along the outer edge of the reef.

The corals, like many other groups of marine organisms, are remarkable for the variety and brilliancy of their color during life. Those who know only the bleached museum specimens have little conception of the living tints, some of rare delicacy, others of brilliant hue. The Hawaiian reefs, although they do not show colors as striking as those of the South Pacific and Indian Oceans, are not lacking in color, and the "Coral Gardens" are becoming far-famed as tourist attractions. Pink, yellow, green, brown, purple and scarlet are represented in many shades and combinations.

One of the most beautiful of the Hawaiian corals is a highly precinctive species, *Dendrophillia Manni*, which is known only from Kaneohe Bay, on the island of Oahu. The living coral is a rich deep orange red. There are numerous short branches, each of which is surmounted by a single bright orange polyp. When fully expanded the polyp is about three quarters of an inch long, and resembles a miniature sea-anemone. The polyp can withdraw completely within its cup. This species is rare,

<sup>3</sup> William Alanson Bryan, "The Natural History of Hawaii," Honolulu, 1915.

occurring only here and there along the margins of the little coral islands in Kaneohe Bay.

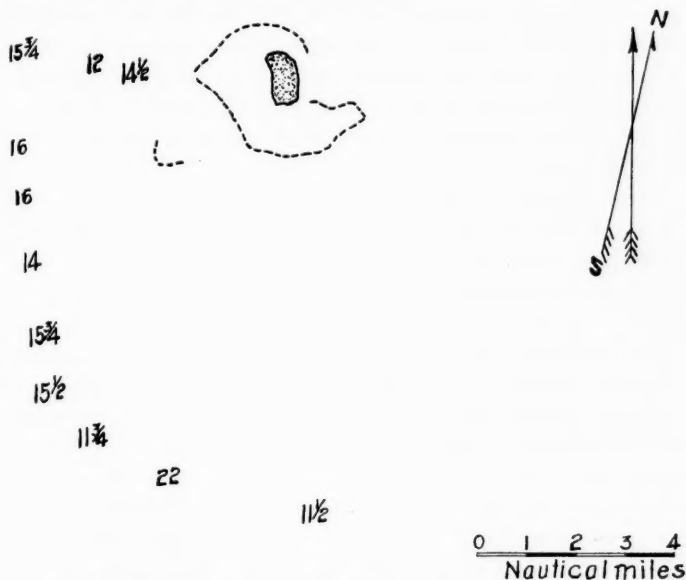


FIG. 4. Lisiansky Island. A low, oval island of coral sand, two miles by three miles; the lagoon empty of water. The surrounding reef extends six or seven miles from the isle.

The famous black coral, *Antipathes abies*, is absent from the Hawaiian reefs, although it has a wide distribution in the Indian and South Pacific Ocean. It grows to considerable size in the tropical waters of the Great Barrier Reef of Australia.

The eight-rayed corals (*Alcyonaria*) are very rare on the reefs, but occur in fair abundance in the deep offshore waters. The *Albatross* collected about 70 new species, 40 of which were new to science. The Red or Precious Coral of commerce, *Corallium rubrum*, does not occur in the Hawaiian Archipelago. It is most abundant in the Mediterranean Sea, although also occurring off the coasts of Ireland and Africa. Related species of slight commercial value have been obtained off Mauritius and near Japan.

The *Alcyonacea*, organ-pipe and blue corals, are represented in Hawaii by only five species; the *Gorgonacea*, sea-fans, by 16 species; and the *Pennatulacea*, sea-pens, by 48 species. Many of the Hawaiian members of these groups are of great beauty, but are never found *in situ* on the reefs, and when rarely washed ashore are badly mutilated by the waves. Some of the species are phosphorescent.

The typical Hawaiian fringing reef exhibits five distinctive biological zones. This zonation parallels the shore-line, and is best developed on those reefs which possess wide lagoons and a well-defined outer margin or rim.

1. *Beach or Inshore Waters*.—The shallow inshore waters, varying in depth from 6 to 36 inches, sustain a number of the quiet-water algæ, such as *Enteromorpha* spp., *Hypnea nidifica*, *Gracilaria*, *Chatomorpha*, *Ulva*, *Chondria*, *Liagora*, etc. The bottom is of coral sand or mud, more or less contaminated by volcanic soil washed from the lowlands. The water is often mingled with relatively high percentages of fresh water. The nature of the bottom depends largely upon the proximity of fresh-water streams and of the reef-rim. In many places where the surf is heavy and reef material abundant, the bottom is pure white coral sand, with practically no rock or mud. In other districts there are large mud-flats exposed at low tide; the limestone pavement is covered with a thin sheet of mud, with little sand. Every gradation may be found between these two extremes. At the mouths of streams and at numerous other places along the coasts where fresh-water springs exist below tide-level, the inshore water is so fresh as to prohibit the development of the strictly marine species.

2. *Partially Submerged Rocks*.—In some places the beach and shallow waters are devoid of rock masses, but in general one finds partially submerged rocks scattered all along the coasts. These may be either close inshore, in the form of ledges or detached fragments, or may lie



at varying distances from the shore. In any case they distinctly indicate, by their horizontal banding of algal and hydroid life, the ranges of high and low tide. The rocks are either of consolidated reef coral or of black basaltic lava; tufa rocks, and sedimentary coral sandstone are infrequent. Some groups of marine organisms show strong preference for the coral rock, others for the lava rock. The rocks may be in somewhat protected situation or may be exposed to the full force of the surf. The following genera contain algæ which are representative of the kinds that withstand the constant battering of the waves: *Gymnogongrus*, *Codium*, *Haliseris*, *Asparagopsis*, *Dictyota*, *Gelidium*, *Ahnfeldtia*, *Porphyra*. The controlling factor in the alga-flora of the partially submerged rocks seems to be the circulation of pure, well-oxygenated sea water. Rocks in stagnant or impure water support a scanty flora as compared with those of the surf-swept localities.

3. *Pools*.—Beyond the rock litter, although sometimes interspersed by it, lies the zone characterized by numerous pools or pockets. These cup-like depressions in the lagoon floor vary in size from little pockets two or three feet in depth and diameter to large pools twenty or thirty feet in depth and diameter. In wading or paddling over the reef, the pools are easily distinguished by the darker tint of their waters as contrasted with that of the shallow lagoon. These pools in the floor of the lagoon are not to be confused with the tidal pools, that lie along the beaches, and are entirely detached at low tide. The lagoon pools are inhabited by a great variety of algæ and animals that prefer these shadowy havens to the exposure of the shallows or the outer reef. The bottom of the pool may be covered with clear coral sand, or coral débris, or masses of living coral; its alga-flora will depend upon its depth and the resultant intensity of illumination.

The following are typical alga genera that have representatives in the lagoon pools: *Corallina*, *Peysonnelia*, *Grateloupia*, *Ceramium*, *Amansia*, *Polysiphonia*, *Chon-*

*dria*, *Laurencia*, *Martensia*, *Champia*, *Wrangelia*, *Galaxaura*, *Padina*, *Sphacelaria*, *Hydroclathrus*, etc.

4. *The Lagoon*.—The entire region between the beach line or strand and the seaward rim of the reef is properly designated as the lagoon, but for the purposes of this description the term will be restricted to the deeper waters, which are usually located about midway between the beach and the reef-rim. As one approaches the lagoon wading becomes impossible, the water deepens to eight, twelve or twenty feet, but again becomes shallow as the outer edge

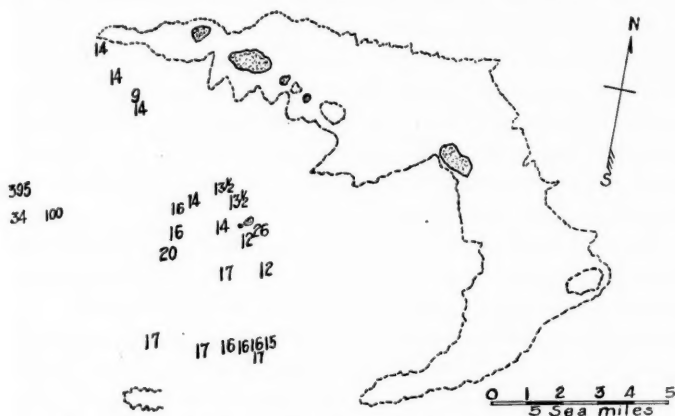


FIG. 5. French Frigates Shoal. Crescentic atoll, with numerous low sand islands, and several high rocky volcanic isles; area of shoal about 30 sq. miles. The reefs are extensive.

of the reef is reached. The water of the lagoon is placid, clear, and in normal weather very translucent, so that the bottom receives good illumination. Although a number of the smaller algæ grow upon the floor of the lagoon, the region is comparatively barren as compared with the shallower waters on either side. The lagoon floor is a region of coralline and animal life, rather than of plant life. The quantities of sand and silt that are constantly washed over the floor from the disintegrating reef-rim render it difficult for plants to maintain themselves. The floor is so irregular in topography that collecting is very difficult;

dredging is almost impossible, and diving is both laborious and unsatisfactory.

5. *Reef-Rim*.—Upon paddling across the lagoon to the outer rim of the reef, one comes to shallow water, where the heavy combers break and where wading is again possible. This zone is a favorite fishing-ground of the native Hawaiians, as it abounds with plant and animal life. The highest portions of the rim are usually exposed at low tide; at high tide they are covered by 18-24 inches of water. There are many table-rocks or shoals, with deep channelways between. The rim is not regular or symmetrical; there are many indentations, crags, debris slopes, pools, hummocks and sandy spots. Almost all of the visible coral of this region is living coral, associated with an abundance of corallines, bryozoans, hydroids and red and brown algæ. Some of the algal genera that are confined largely to the outer reef-rim are: *Codium*, *Asparagopsis*, *Gymnogongrus*, *Porphyra*, *Turbinaria*, *Dictyota*, *Haliseris*, *Gelidium*, etc. Many of the species that inhabit these turbulent and surf-churned waters are not the tough, cartilaginous forms, but are very delicate and fragile species, that apparently survive the wave action because of their very delicacy. This is particularly true of some of the finer red algæ.<sup>4</sup>

Highly important on the Hawaiian reefs are the coralline or stony algæ or nullipores. A number of genera—

<sup>4</sup> Some of the representative marine algæ of Hawaii that are common on the coral reefs and shallows are: *Oscillatoria bonnemaisonii*, *Phormidium crosbyanum*, *Lyngbya semiplena*, *L. majuscula*, *Hydrocoleus cantharidosmus*, *Nodularia Hawaiiensis*, *Hormothamnion solutum*, *Scytonema fuliginosum*, *Calothrix æruginea*, *Ulva* spp., *Enteromorpha* spp., *Chaetomorpha pacifica*, *Cladophora* spp., *Bryopsis plumosa*, *Caulerpa taxifolia*, *Halimeda* spp., *Codium* spp., *Falonia* spp., *Dictyosphaeria favulosa*, *Microdictyon umbilicatum*, *Ectocarpus* spp., *Sphacelaria* spp., *Hydroclathrus cancellatus*, *Asperococcus bulbosus*, *Turbinaria ornata*, *Sargassum* spp., *Padina pavonia*, *Dictyota* spp., *Liagora decussata*, *Galaraura lapidescens*, *Scinaia furcellata*, *Gelidium* spp., *Wrangelia penicillata*, *Gymnogongrus* spp., *Ahnfeltia concinna*, *Gracilaria* spp., *Hypnea nidifica*, *H. armata*, *Plocamium sandwicense*, *Martensia flabelliformis*, *Asparagopsis sanfordiana*, *Laurencia* spp., *Chondria tenuissima*, *Polysiphonia* spp., *Amansia glomerata*, *Ceramium* spp., *Grateloupia flicina*, *Peyssonnelia rubra*, *Corallina* spp., *Lithothamnion* spp.

*Lithothamnion*, *Corallina*, *Mastophora*, and others—are abundant on the reefs, and undoubtedly have been active as reef-builders. The importance of the lime-secreting algæ was overlooked by the earlier students of coral reefs, but is now receiving adequate consideration. Howe<sup>5</sup> shows that these forms work effectively at greater depths and at lower temperatures than do the true corals, and that they are much more generally and widely distributed than the latter.

The Hawaiian coralline algæ inhabit the shallow waters, as well as occurring at considerable depths. In the former situations they form beautiful rose, purple and lavender incrustations. On the faces of cliffs that are washed by the sea these incrustations appear as conspicuous bands, extending from high-tide mark or the uppermost wash of the surf down to the zone of minimum illumination. The lower margin of the coralline zone has not been investigated in the Hawaiian Islands, but in other island groups they flourish at 1,000 ft. depth. In the coralline zone are also many of the calcareous hydrozoa.

Sponges of many species, sizes and colors abound in all protected portions of the reefs, but have never been made the subject of critical taxonomic study. They range from tiny, fragile forms, the size of a shoe-button, up to coarse horny masses as large as a man's head. The lesser species are common on the coral-rock litter in the lagoons. The larger forms inhabit the deeper waters, and are torn from their anchorage only by the occasional severe storms. After a period of southerly storms, for example, the leeward beaches are littered with these large, tough sponges, which average eight inches in diameter.

The range of color is bizarre and striking. In a single afternoon's collecting one may pick up, in the shallow water, species of bright red, pale yellow, rich purple, dull brown, creamy white, green, and dead black pigmentation. Dredging reveals others which add to the chromatic series. Most of the sponges are of the encrusting type, the body

<sup>5</sup> M. A. Howe, "Building of Coral Reefs," *Science*, 36: 837-842, 1912.

conforming to the substratum and having no definite shape. The *Calcarea* are not uncommon in the littoral region, especially in sheltered situations among rocks and seaweed. These and the true horny sponges (*Ceratosa*) have not been found below 2,700 ft. The sponges found at the greatest oceanic depths are members of the *Hexactinellida* and *Choristida* of the *Non-Calcarea*.

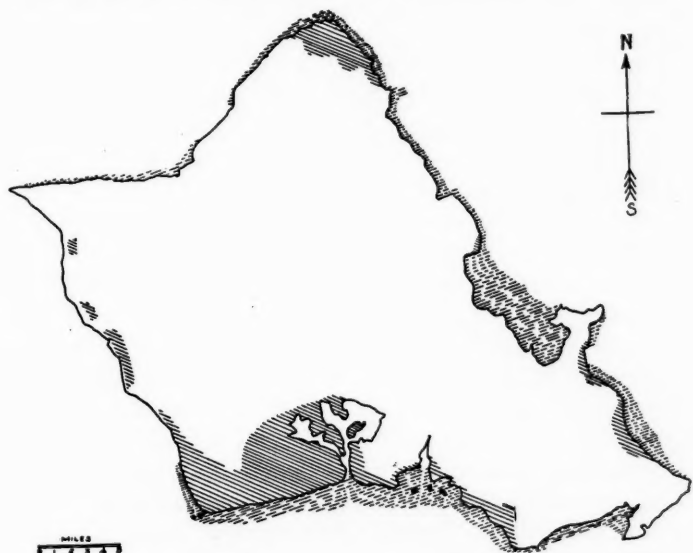


FIG. 6. Island of Oahu. Showing extensive development of coral reefs // and elevated coral limestone ///. Note the abundance of coral in the vicinity of Pearl Harbor (the fan-shaped bay on the south coast), Kaneohe Bay (on the northeast coast) and along the southern shores.

The Hawaiian sponges have few or no natural enemies, and do not appear to be edible to fishes, crustaceans or molluscs. Innumerable lowly forms, however, inhabit their tissues, for shelter, if not for food. The interior of any one of our common reef sponges is almost sure to be found teeming with minute crustaceans, annelids, molluscs and other invertebrates.

None of the Hawaiian species have been utilized commercially and no serious attempts have been made to in-

roduce and establish the valuable species from other parts of the world. All of the commercial sponges belong to the two genera *Euspongia* and *Hippospongia*, which do not occur on the Hawaiian reefs. Such an enterprise, if undertaken with thorough scientific supervision, would unquestionably meet with success. There are many areas along our reefs where the sponges could be established. With adequate labor and marketing arrangements a steady development of the industry would be assured.

It is of interest to note that of the fresh-water sponges, *Spongillinae*, a group which is widely distributed in all parts of the world, no representatives have been taken in the Hawaiian Islands.

Jellyfish are of casual occurrence along our reefs. The smaller forms are chiefly Hydrozoan medusæ; the larger ones are Scyphozoans. A relatively few species are known and the life-cycles of these are not known in detail. A number of the tiny species are phosphorescent, and on clear nights when the sea is calm and other conditions are favorable, they give beautiful luminous effects. In paddling along the reef in an outrigger canoe, on such a night, the paddles, at every stroke, drip with tiny stars. Many of the larger species have gonads, tentacles, radial canals, or other organs brilliantly pigmented.

The large forms attain diameters of 8-12 in. and sometimes appear in great numbers in quiet, protected waters. Pearl Harbor, for example, which is almost wholly landlocked, is a favorite habitat. At low tide, in other parts of the islands, along the coral beaches one sometimes finds great numbers of jellyfish stranded and slowly deliquescing.

In addition to the true jellyfish the reefs support a rich hydrozoan or marine hydroid fauna. The littoral species have not been studied taxonomically; the *Albatross* collections were made at depths of 60-3,000 ft. These latter comprised 49 species, representing 27 genera and 11 families. The shallow-water zoophytes or hydroids are abun-

dant in all protected situations; many forms also inhabit the surf-beaten rim. *Sertularia*, *Plumularia* and *Campanularia* are well-known genera. The species are all of small size and superficially resemble in habit, color and habitat the more delicate marine algæ.

The false corallines or *Hydrocorallinae* are also very abundant and have played an important rôle, as have the coralline algæ, in the construction of the Hawaiian reefs. These colonial animals resemble delicately branching corals; their bleached and rather fragile skeletons are common on the beaches. When alive the corallines are of various tints of pink, orange and salmon, and add bright touches of color to the brilliant ensemble of the reef. The *Hydrocorallinae* occur only in tropical seas; *Millepora* and *Stylaster* are typical genera.

That remarkable order of free-floating colonial hydroids, the *Siphonophora*, is well represented in all tropical waters, and has numerous forms in the Hawaiian marine fauna. This group exhibits the greatest diversity of form. The common "Portugese man-of-war," *Physalia utriculua*, with its brilliant peacock-blue float and long retractile tentacles, is abundant along the reefs and shallows, and like the jellyfish, is often cast ashore in enormous numbers. The tentacles contain powerful batteries of stinging capsules; the wounds are intensely painful, and so this lovely evanescent creature is dreaded by bathers. Other well-known genera are *Halitemma*, *Diphyes*, *Porpita* and *Vellelo*. *Porpita pacifica*, the sea-money, is a beautiful blue-fringed disc about  $1\frac{1}{2}$  in. in diameter. *Vellela pacifica* is also abundant at certain seasons. It resembles *Physalia*, but has much shorter tentacles.

Sea-anemones, *Actiniaria*, are abundant along the Hawaiian reefs, but no taxonomic studies have been made. A number of species inhabit the inshore pools whose waters are periodically renewed by waves or tides; others may be found on the floor of the lagoon, and still others on the protected sides of rocks which stand in the heavy

surf. The colors most frequently observed are shades of tan, olive and purple; some forms have tentacles which are beautifully pigmented. The size varied from species so minute as to almost escape detection up to fine showy forms 1-2 in. in diameter. They form considerable colonies, sometimes covering areas of several square feet. Isolated individuals, particularly of the larger species, are not rare. Usually their rosette of tentacles and brilliant color renders them quite conspicuous, but many kinds are embedded more or less completely in the substratum, and upon the slightest alarm contract into shapeless lumps, and are thus easily overlooked.

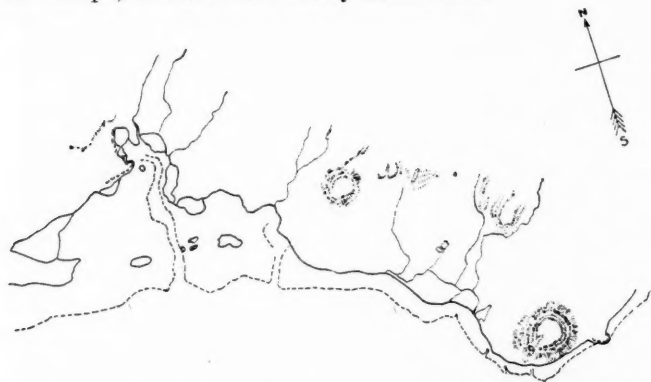


FIG. 7. Coral Reefs near Honolulu, Oahu. The city of Honolulu is built upon a limestone plain. The coral reefs which extend along the coast are well developed and very rich in plant and animal life. There are numerous evidences of repeated subsidence and elevation. The crater on the right is Diamond Head (Leahi); the channel to the left is Kalihi Channel. Honolulu Harbor is the middle channel.

The *Ctenophora* have about 20 known species in Hawaiian waters, but these are so rare and fragile that they are practically unknown to the reef-collector. They are all pelagic, delicate, transparent creatures, with long tentacles and peculiar comb-like locomotor organs. As they swim gently through the sunlit waters their transparent bodies and tentacles yield beautiful iridescent reflections. *Hormiphora*, *Cestus*, and *Beroë* are well-known genera. All the members of this highly specialized group are solitary and do not form skeletons.



The fauna which inhabits the innumerable small cavities in the coral, and which drills countless tunnels through the soft rock, is of much interest. This fauna comprises chiefly the worm-like animals or sea-worms. Important groups are *Turbellaria*, *Nemertinea*, and *Annelids*. Some species creep about in the interstices; others construct covered passageways on the surface of the coral. Others burrow in the sand and mud on the floor of the lagoon. Some tunnel deviously through the coral rock itself. Many of the sea-worms are brightly colored. Little is known concerning the relationships or life-histories of the Hawaiian forms. *Nereis*, *Serpula*, *Terebella*, *Tubifex*, *Sipunculus*, and *Echiurus* are characteristic annelid genera.

The true corallines (*Polyzoa*) or sea-mats bear a close resemblance to the hydroid zoophytes, and only upon microscopic inspection show that their organization is much higher than that of the hydroids. The skeleton is not exclusively calcareous; in many forms it is chitinous or even gelatinous. These corallines are abundant on the Hawaiian reefs.

The true starfishes, *Asterioidea*, are comparatively rare on the reefs themselves, although fairly common in the offshore waters. The brittle-stars, *Ophiuridea*, are the common reef forms, and lurk in every cranny. The *Albatross* expedition collected 60 Hawaiian species of true starfish during its dredging operations in the island channels; they were taken at depths of 60-6,000 ft. These represented 46 genera and 20 families; 52 species were new to science. According to Bryan,

Large specimens of an eight-rayed starfish, *Luidia hystrix*, are occasionally captured at Pearl Harbor. They are often a foot and a half in diameter. A similar but very small species is to be found abundantly in the coarse green sponges in Kalihi Bay and at Pearl Harbor. A small, stiff, irregularly developed, pink, leather-like species, *Linckia* sp. without spines, is occasionally found crowded into small holes in the coral reef.

The common brittle-star, *Phiæma* sp., is blue-black in color, with small body and long snaky arms. It is gre-

gamous in habit, and the collector frequently finds a dozen or more congregated beneath a half-buried stone or coral mass. A tiny pink species, *Ophiothrix* sp., with remarkably long arms, inhabits crevices in the coral. It is very difficult to capture intact, because it, like most of the Ophiuroids, possesses to a remarkable degree the faculty of self-mutilation. Many of the Hawaiian brittle-stars, when disturbed or removed from the water, sever portions of their arms piece by piece until finally nothing is left but the central disc. This is capable of developing a new set of arms; and a detached arm can, under favorable conditions, develop a new disc and a completed series of arms. The basket-stars, *Cladiophiura*, have never been collected on the Hawaiian reefs.

The sea-urchins, *Echinoidea*, are richly represented, but most of the species inhabit the deep offshore waters. The inshore species are gregarious and common in all rocky situations along the coasts, as well as on the reefs themselves. *Podophora pedifera*, for example, prefers the black lava rocks and cliffs exposed to the full force of the surf, and is so abundant that the zone of massive basalt which it inhabits is literally honeycombed with its burrows. Several species of *Echinometra* are also very abundant; these prefer the shallow waters of the lagoons. In the deep holes and caverns along the outer edge of the reef is a large purple-black species, *Diadema paucispinum*, with slender, awl-shaped spines. In the same situations occurs *Echinothrix desori*, a large form whose long spines are beautifully banded with gray and black. The curious club-spined urchins, *Heterocentrotus* spp., occur here and there along the reef, and are frequently exhibited in the Honolulu Aquarium. The sea-biscuit, *Brissus carinatus*, is a large, heart-shaped urchin, covered with short, brown hair-like spines, and is occasionally found along the reef rim. A number of the Hawaiian urchins are known to the natives as *wana*, or "sea-eggs," and are habitually used by them for food. They may be purchased in the local fish markets.

Numerous species of holothurians (known as sea-cucumbers, sea-squirts, and *bêche-de-mer*) are common in the shallow waters. There are over 40 described species, representing 4 families and 21 genera. A large, worm-like form, *Opheodesoma spectabilis*, is common at Pearl Harbor and Kaneohe Bay, in quiet water. It is about 2 ft. long and  $1\frac{1}{2}$  inch diameter, reddish brown mottled with brown. A large, dark greenish-brown species, *Stichopus tropicalis*, is plentiful in the large pools of the outer reef, near Honolulu. Inhabiting the tidal pools in the lava rocks is another large form, *Holothuria atra*; dark brown, and with ambulacral feet scattered all over its body. Frequently associated with it is a heliotrope-purple species, *Holothuria cinerascens*. There are about 600 known species of holothurians, varying in size from  $\frac{1}{2}$  inch to 2 or 3 feet. They are found in all seas, but are particularly abundant in the West Indies, and between Asia and Australia. They feed chiefly on Foraminifera. The movements of all the Hawaiian species are very sluggish; they seem to have few enemies. All are harmless, although of unpleasant aspect. They are capable of the most extraordinary regeneration of parts, even of the most important organs. Many species show the curious habit of evisceration—when alarmed they dispel from the anal opening the viscera either wholly or in part. In the course of a few weeks all of the lost organs are replaced by a new set.

The Crinoids or sea-lilies do not exist in the shallow waters of the Hawaiian reefs. A dozen forms were collected by the *Albatross* at depths of about 600 ft. These all proved to be new species, although representing 8 wide-ranging genera in 4 families of the non-stalked *Neo-Crinoidae*. Crinoidal fossils have not been found in the uplifted coral limestone beds of the Hawaiian Archipelago. These forms made important contributions to the Silurian and Devonian rock strata in other parts of the world, during which epochs the crinoids were enormously abundant.

Molluscs abound on all the reefs. There is a tremendous range of size, structure, habitat and generic representation. The marine molluscan fauna has never received adequate attention, as scientific interest has centered upon the unique terrestrial and arboreal forms. There are about 20 species of bivalves (*Pelecypoda*) that are fairly common. These include such genera as *Mytilus*, *Perna*, *Arca*, *Ostrea*, *Anomia*, *Pecten*, *Tellina*, *Cadokia*, *Cytherea*, *Venus*, *Cardium* and *Chama*. *Tellina sugosa*, the *Olepe*, is, according to Bryan, "the most important shell-bearing mollusc" in the islands. The famous pearl shell, *Avicula margaritifera*, of the South Pacific, does not occur in Hawaiian waters. The Hawaiian pearl oyster, *pa*, *Margaritifera fimbriata*, has a shell often 3 or 4 inches broad, with a brilliant iridescent interior. It is the species which gave Pearl Harbor its name. In the early days the collecting of *pa* was a royal monopoly, like the collecting of sandalwood. The pearl-shell was used by the Hawaiians chiefly for making fish-hooks, and for the curious shell-eyes of their wooden gods. A true pearl-bearing species also occurs at Pearl Harbor and other localities in the group in the deeper offshore waters. The edible oysters are represented by *Ostrea rosea*, which is not of sufficient abundance to permit commercial exploitation.

The chitons and their allies, *Amphineura*, are uncommon in the shallows, but a thorough systematic survey would undoubtedly bring to light many additional forms. The true chitons, *Placophora*, are confined largely to the shallows, and apparently are herbivorous, feeding on minute algæ and diatoms. The *Aplacophora* as worm-like, shell-less creatures, with the body beset with calcareous spicules. They are wholly absent from the littoral zone, occurring only at considerable depths—3,000 ft. and in some instances down to 7,500 ft. They are carnivorous and subsist on such small animals as hydroids and coral polyps.

The univalves or Gasteropods are by far the most

abundant molluscs on the Hawaiian reefs and aggregate several hundred species. Space forbids any detailed treatment of this huge and highly diversified class. A bare enumeration of important and common families and genera, adapted from Bryan, will indicate the richness of the marine univalve fauna (the number of species is in each instance an approximation):

Family	Species	Typical Genera
Tritons; Tritonidae .....	12	<i>Triton, Ranella.</i>
Spiny Rock Shells; Muricidae ..	30	<i>Purpura, Ricinula, Vexilla, Sistrum.</i>
Spindle Shells; Fusidae .....	6	<i>Fusus, Latirus, Peristernia.</i>
Whelks; Buccinidae .....	6	<i>Pisania, Cantharus.</i>
Dog Whelks; Nassidae .....	4	<i>Nassa.</i>
Mitre Shells; Mitridae .....	26	<i>Mitra, Imbricaria, Turricula.</i>
Margin Shells; Marginellidae ...	4	<i>Erato, Marginella.</i>
Olive Shells; Olividae .....	4	<i>Harpa, Oliva.</i>
Dove Shells; Columbidae .....	15	<i>Columbella, Engina.</i>
Cone Shells; Conidae .....	25	<i>Conus.</i>
Auger Shells; Terebridae .....	25	<i>Terebra.</i>
Conch Shells; Strombidae .....	9	<i>Strombus.</i>
Cowry Shells; Cypræidae .....	40	<i>Cypræa, Trivia.</i>
Tun Shells; Doliidae .....	2	<i>Dolium.</i>
Cameo Shells; Cassidae .....	5	<i>Cassis.</i>
Moon Shells; Naticidae .....	10	<i>Natica.</i>
Slipper Shells; Calyptraeidae ....	12	<i>Crepidula, Crucibulum, Hipponyx.</i>
Eulimas; Eulimidae .....	17	<i>Eulima.</i>
Pyramid Shells; Pyramidellidae. 3		<i>Pyramidella.</i>
Sun-dial Shells; Solariidae .....	6	<i>Solarium.</i>
Violet Snails; Ianthinidae .....	3	<i>Ianthina.</i>
Ladder Shells; Scalariidae .....	10	<i>Scalaria.</i>
Herald's-horn Shells; Cerithiidae	20	<i>Cerithium.</i>
Periwinkles; Littorinidae .....	3	<i>Littorina, Modulus, Risella.</i>
Sea-Snails; Neritidae .....	10	<i>Nerita, Neritina.</i>
Turban Shells; Turbinidae .....	18	<i>Turbo, Phasianella, Astralium.</i>
Top Shells; Trochidae .....	12	<i>Trochus.</i>
Limpets; Fissurellidae and Patel- lidae .....	10	<i>Helcioniscus.</i>
Sea Slugs; Nudibranchiata ....	10	<i>Aplysia.</i>

The highest and most highly specialized class of molluscs, the Cephalopods, have an abundant and familiar representative on our reefs, in the form of the common octopus or *he'e*. This is popularly called "squid" although it is a true cuttlefish, with a small round sac-like body and eight arms. It is very common in holes and

pools on the rocky platform of the reef, and in caverns along the reef-rim. During the day it hides in cavities; at night it creeps about over the rocks of the bottom. The natives are very fond of the flesh, which they prepare for food in a variety of forms. Dried "squid" is common in the fish-markets. Our cuttlefish is rarely more than 18-26 inches in length. The true "devil-fish" of many a sea-tale is a giant squid, *Architeuthis*, which inhabits the Newfoundland banks and often attains the gigantic proportions of an over-all length of 50 ft., with a body 6 by 9 ft., and enormous arms 40 ft. long.

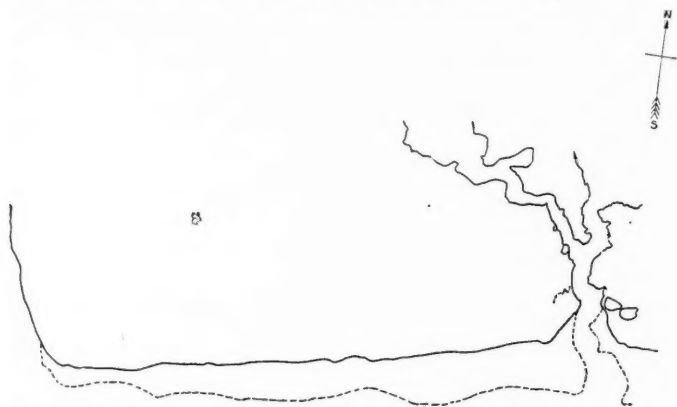


FIG. 8. Coral Reefs near Pearl Harbor, Oahu. The inlet to Pearl Harbor is shown to the right. To the left is the southwest point (Barber's Point) of the island. The lowland is a plain of coral limestone; the reef is rich in biological material.

Our reefs support a characteristic crustacean fauna. In the growing coral at the reef-edge are found a number of small Cyclometopous crabs, which are often beautifully sculptured and colored to harmonize with the coral. The *Alpheidae*, which are shrimp-like *Macrura* with highly asymmetrical claws, are commonly found in pools on the reef. In the coral rubble formed by the disintegration of the reef-rim, in relatively shallow water, numerous Leucosiid crabs are found. Many lowly forms of Entomostraca are abundant, but have never been surveyed

taxonomically. The Phyllopods, Ostracods and Copepods are all plentiful. The Cirripedia include the most aberrant of the crustaceans, and are represented by the common barnacles, including both the stalked (*Lepadidæ*) or goose barnacles, and the sessile (*Balanidæ*) or acorn-



FIG. 9. Kaneohe Bay, Oahu. This bay, which is a drowned valley complex, has a great variety of coral formations. There are many small coral isles and atolls; some are of notable perfection. The exact boundaries of the outer reefs are not known. The crater and little isles to the lower right are secondary volcanic products.

shells. The latter are exceedingly abundant along the shores and reefs; there are also numerous deep-water barnacles.

The most commonly known, the largest and the most highly organized crustaceans, the Malacostraca, are very common. Space does not permit even a general sketch of the many crabs, prawns, crayfish and other interesting forms that teem in the Hawaiian littoral. The so-called Hawaiian "lobster," *ula*, *Panulirus japonicus*, is really a large marine crayfish, and not closely related to the true lobster. It is brilliantly colored and ornamented, with spiny carapace and long antennæ. The *ula* is common in the fish markets, as are also species of *Scyllarides*, *Ocy-poda*, and many crabs. Hermit crabs (*Onomura*) are common and in great variety. They make their homes in empty sea-shells, and have many interesting habits.<sup>6</sup>

The last great division of the reef fauna comprises the fishes, a group that could easily occupy the space of an extended monograph. There are several hundred reef species, occupying a wide range of habitats, and varying in size from minute species up to huge food-fish weighing a hundred pounds each. Like the fish of many tropical waters, the Hawaiian species are famous for their brilliant coloration, fantastic patterns, and strange shapes. Many are grotesque; many are exceedingly beautiful; many are consummate embodiment of that riot of gorgeous color that is so characteristic of the reef and its life. The reef fishes, like the other littoral forms of life, were an important item in the dietary of the primitive Hawaiians, and continue so to the present day. Most of the common species are offered for sale in the fish-markets. Space is not available for any detailed account of the in-

<sup>6</sup> The following list of common littoral and reef species and genera of malacostraceans will indicate the richness of this portion of Hawaii's remarkable reef fauna: I. *Brachyura*—*Ocypode ceratophthalma*, *O. lævis*, *Grapsus grapsus*, *Metopograpsus messor*, *Pachygrapsus plicatus*, *Cyclograpsus*, *Percnon*, *Carpilius*, *Platypodia*, *Lophozozymus*, *Xantho*, *Leptodius*, *Xanthodius*, *Etisus*, *Actæa*, *Chlorodiella*, *Phymodius*, *Grapsillus ferrugineus*, *Polydectus cupulifer*, *Portunus*, *Charybdis*, *Thalamita*, *Podophthalmus*, *Simocarcinus simplex*, *Calappa*; II. *Macrura*—*Scyllarides*, *Patemonella*, *Parribacus*, *Panulirus*, *Stenopus*, *Penæus*, *Hippolyasmata*, *Spirontocaris*.



shore<sup>7</sup> fishes, as contrasted with the pelagic and abyssal species.

<sup>7</sup> Some of the more important groups and species may be listed as follows:

Sharks .....	<i>Carcharias melanopterus</i> ; <i>C. nesiotes</i> ; <i>Sphyrna zygaena</i> ; <i>Isuropsis glauca</i> .
Rays .....	<i>Stoasodon narinari</i> .
Tarpons .....	<i>Elops saurus</i> .
Bonefishes .....	<i>Albula vulpes</i> .
Milkfishes .....	<i>Chanos chanos</i> .
Anchovies .....	<i>Anchovia purpurea</i> .
Lizardfishes .....	<i>Trachinocephalus myops</i> ; <i>Synodus varius</i> ; <i>Saurida gracilis</i> .
Conger Eels .....	<i>Leptocephalus marginatus</i> .
Morays .....	<i>Muraena</i> , <i>Enchelynassa</i> , <i>Gymnothorax</i> , <i>Eurymyctera</i> , <i>Echidna</i> , <i>Uropterygius</i> , <i>Scuticaria</i> .
Trumpetfishes .....	<i>Aulostomus valentini</i> .
Coronetfishes .....	<i>Fistularia petimba</i> .
Needlefishes .....	<i>Athlennes hians</i> .
Half-beaks .....	<i>Hemiramphus depauperatus</i> ; <i>Euleptorhamphus longirostris</i> .
Flyingfishes .....	<i>Parexocetus brachypterus</i> ; <i>Cypsilurus simus</i> ; <i>C. bahiensis</i> .
Friars .....	<i>Atherina insularum</i> .
Mulletts .....	<i>Mugil cephalus</i> .
Barraudas .....	<i>Sphyræna helleri</i> .
Threadfins .....	<i>Polydactylus sexfilis</i> .
Squirrelfishes .....	<i>Holotrachys lima</i> ; <i>Myripristis</i> spp.; <i>Flammeo samarra</i> ; <i>F. scythrops</i> ; <i>Holocentrus</i> spp.
Big-eyed Scads .....	<i>Trachurops crumenophthalma</i> ; <i>Carangus</i> .
Threadfishes .....	<i>Alectis ciliaris</i> .
Cardinalfishes .....	<i>Mionorus</i> , <i>Foa</i> , <i>Amia</i> .
Groupers .....	<i>Epinephelus quernus</i> .
Catalufas .....	<i>Priacanthus</i> .
Snappers .....	<i>Apsilus</i> , <i>Aphareus</i> , <i>Bowersia</i> , <i>Aprion</i> , <i>Etelis</i> .
Porgies .....	<i>Monotaxis grandiculis</i> .
Rudderfishes .....	<i>Kyphosus</i> .
Surmulletts .....	<i>Mulloides</i> .
Goatfishes .....	<i>Pseudupeneus</i> ; <i>Upeneus</i> .
Demoiselles .....	<i>Dascyllus</i> ; <i>Chromis</i> ; <i>Pomacentrus</i> ; <i>Abudefduf</i> .
Wrassefishes .....	<i>Lepidaplois</i> ; <i>Stethojulis</i> ; <i>Halichoeres</i> ; <i>Gomphosus</i> ; <i>Anampses</i> ; <i>Thalassoma</i> ; <i>Julis</i> ; <i>Coris</i> ; <i>Cheilio</i> ; <i>Cheilinus</i> ; <i>Novaculichthys</i> ; <i>Iniistius</i> ; <i>Hemipteronotus</i> ; <i>Xyrichtys</i> .
Searids .....	<i>Calotomus</i> ; <i>Callyodon</i> .
Butterflyfishes .....	<i>Forcipiger</i> ; <i>Chaetodon</i> ; <i>Holocanthus</i> .
Moorish Idols .....	<i>Zanclus canescens</i> .
Surgeonfishes .....	<i>Hepatus</i> , <i>Zebрасoma</i> , <i>Ctenochaetus</i> , <i>Acanthurus</i> , <i>Calli-canthus</i> .

The gorgeous colors of many of our reef fishes are very evanescent, and undergo rapid deterioration when the fish is taken from the water. Hence the coloration of those offered for sale in the markets often conveys but little idea of their living hues. Preserved specimens and printed descriptions are of even less value.

In concluding this condensed sketch of the Hawaiian reefs, the writer desires to emphasize his impression of the struggle for life which goes on there unceasingly. The reef is a region of intense competition. It is comparable in many of its ecologic relations to the montane rain-forest. The excessive illumination of the reef is perhaps as constraining an influence as is the excessive humidity of the rain-forest. The diversity of organisms which inhabit the reef is far greater than that of any other island habitat. The competition for food is keen and unremittent.

The reef as a food supply for human beings has been a dominant factor in the lives of the primitive Polynesians. Through the experiences of thousands of years they have acquired a very intimate knowledge of the reef and its life, but this has never been given adequate scientific investigation. One of the great forward steps in the economic history of the world will be the scientific utilization of coral reefs and their products.

Triggerfishes	.....	<i>Balistes, Balistapus, Stephanolepis.</i>
Puffers	.....	<i>Tetraodon, Canthigaster.</i>
Trunkfishes	.....	<i>Ostracion, Lactonia.</i>
Cirrhitoid fishes	....	<i>Paracirrhites, Cirrhites.</i>
Mail-cheeked fishes	..	<i>Caracanthus.</i>
Scorpenids	.....	<i>Sebastapistes, Sebastopsis, Scorpenopsis.</i>
Gobies	.....	<i>Eleotris sandwicensis, Asterropteryx semipunctatus,</i> <i>Eviota epiphanus, Gobiomorphus eugenius, Mapo</i> <i>fuscus, Gobiichthys, Gnatholepis knighti.</i>
Blennies	.....	<i>Enneapterygius atriceps, Alticus, Enchelyurus, Sala-</i> <i>rias.</i>

# CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS. III

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## VII. MUTATIONS

In a recent paper (1917a) I have described two widely aberrant color types which have appeared in my cultures, together with certain minor deviations, which likewise seem to behave as discontinuous variations. I am prepared to add considerably to the data thus far published.

### 1. "*Partial albinos*"

The term albino, as applied to these mice, admittedly does not conform to current usage, and this has become especially evident with the appearance of the mature pelage. I do not think, however, that any of the various names given to fancy races of *Mus musculus* apply to these animals. Having at hand no specimens or even satisfactory colored plates of fancy mice, I am unable to make the comparisons.<sup>27</sup> As previously stated, this mutant strain has red eyes, and lacks pigment wholly on the ears and tail. The fur, on the colored region of the body, is a very pale gray, rather strongly tinged with a shade of yellow approaching Ridgway's "ochraceous buff," or perhaps "ochraceous orange," on the most highly colored areas. As a convenient non-committal expression, I shall henceforth employ the term "pallid" for these mice."

A microscopic examination of the hairs of these mice reveals some interesting departures from the normal condition:<sup>28</sup> (1) a considerable proportion of the hairs are practically devoid of pigment in the zone which is ordinarily yellow, while the rest are normal in this respect;

<sup>27</sup> It may be that the factional modifications of my mice are the same as those of Castle's "red-eyed yellow" rats (see Castle and Wright, 1915).

<sup>28</sup> Cf. Morgan's account (1911) of the hair of some "modified" individuals of *Peromyscus leucopus ammodytes*.

(2) the surface pigment of the terminal portion of the hairs is nearly or quite lacking; (3) in the basal zone, the black pigment bodies are represented by small flocculent dark masses. Thus, we are not, as in the next "mutant" to be described, merely dealing with changed proportions of perfectly normal types of hair. These red-eyed mice possess types which I have not found in any of the rest of my stock.

At the time of my earlier description of these pale sports, no young had been obtained, but their pedigree suggested that they were simple Mendelian recessives. This conjecture has thus far been sustained. The two "mutants," bred to one another, have given six pale young, like themselves, and no others. When bred to dark mates, of the same stock as themselves (*sonoriensis-rubidus* hybrids), the pallid animals gave only dark young, except in a single instance where the dark parent was known to be heterozygous. In this case, one pallid mouse was the outcome. Of the dark progeny, three broods, aggregating eleven individuals, have thus far been born.

This clear-cut and typical example of Mendelian segregation, in respect to these *mutant* characters, is in striking contrast to the complete lack of segregation—so far as is obvious—in respect to the *subspecific* characters which have entered into the germinal constitution of these same individuals.

As I have previously stated, these parent "mutants" were the offspring of  $F_1$  *sonoriensis-rubidus* hybrids. In a recent article (1917) the Hagedoorns have described a number of strongly aberrant types of rats (including some waltzers!) which appeared in a mongrel strain resulting from the crossing of *Mus alexandrinus*, *M. tectorum* and *M. rattus*. The authors recognize in these aberrant derivations some entirely new products, though they do not attribute their origin to real mutation. In the opinion of the Hagedoorns, as I understand it, these apparently "mutant" characters have resulted, in each case, from the chance coming together of two recessive factors (or two "absences," according to the prevailing

theory). No two of these "absences" coexisted in the gametes of any one of the parent species, and no single "absence" by itself is believed to be adequate to produce one of the abnormalities. Since the average number of each kind of "mutant" in their stock of 37 was approximately 1 in 16, they assert:

These numbers make it clear that we are not dealing with a sort of period of mutation; it was easy to see that the new types were already given in the genotype of the three species crossed (p. 415).

And in later passages the authors generalize this conjecture, as for example:

The only cause for inheritable variability in multicellular organisms which can be of any account in evolution is mating between individuals of unequal genotype, crossing in the widest sense (*Amphimixis*) (p. 418).

That the Hagedoorns's explanation does not fit the case of my pallid *Peromyscus* is evident from the history of the stock. I have obtained, in all, 47  $F_2$  offspring from the mating of  $F_1$  *sonoriensis-rubidus* hybrids, counting only those animals which lived long enough to reveal their essential color characters. These were the progeny of six different fathers and eleven different mothers. Just four of these very pale sports have appeared in my  $F_2$  stock. They are the offspring of a single father by two mothers, both his own sisters. These mothers, by the same father, also produced seven dark young.

It seems plain, therefore, that the mutation in question is not due to any recombination of factors (or their "absences") regularly occurring in the parent races. If it were, we should reasonably have expected similar aberrations among the offspring of other parents. It is hard to determine from their published statement the exact pedigree of the Hagedoorn's aberrant rats. But one thing seems plain. All were the progeny of a single father by two mothers, the latter apparently being sisters. The authors are certainly not warranted, therefore, in assuming that such results would have been obtained by mating *any* animals of the same racial composition.

I am inclined to think that my pale red-eyed mice are true mutants, *i. e.*, that they appeared *de novo* in my cul-

tures. It is more than possible, likewise, that the hybridization of such diverse strains was the disturbing element that led to the loss or modification of a "gene." The latter possibility is strengthened by a consideration of the Hagedoorns's waltzing rats and abnormalities of coat color. But this is a very different view from the hypothesis that "the new types were already given in the genotype of the . . . species crossed."

## 2. *Yellow gambeli*

The five normally colored progeny of a single pair of normally colored *Peromyscus maniculatus gambeli* (La Jolla race) became the parents of 21 offspring, of which 14 were normally colored and 7 were of a peculiar yellowish-brown color. These "mutants," which I have called "yellows," are of a shade not very far removed from Ridgway's "clay color." They are considerably darker than some, at least, of the yellow races of *Mus musculus*. Microscopic examination of the hair of these aberrant *gambeli* shows that it is closely similar to that found upon the more highly colored parts of *P. m. sonoriensis*. In comparison with normal specimens of its subspecies the mutant strain is found to have a larger number of the yellow-banded hairs, in proportion to those which are black throughout their entire length. The latter type of hair is, however, by no means wanting. In the second place, the yellow zone of each hair, on the colored parts of the body, occupies, on the average, a considerably larger proportion of its length. On the mid-ventral surface, the basal, plumbeous zone is quite lacking, the hairs being entirely white. Besides the differences stated, I can not be certain of any hair characters which distinguish this type of sports from the normal stock. Moreover, the eyes, ears, tail, etc., carry a normal amount of black pigment.

It is to be noted that these "yellow" mice, unlike the "partial albinos," are not distinguished by any types of hair which are lacking in normal individuals. We may, however, very justly regard the yellow condition as having arisen through "discontinuous variation." Though due

merely to a change in the proportion of elements previously present, the new type has arisen abruptly and has diverged so widely that its range of variation does not overlap that of the normal race. Among the many hundreds of individuals which I have dealt with, I have never found any mice which would serve in a true sense to bridge the gap between these two types. Nor have any other yellows appeared in my cultures, except among the descendants of the single pair in question.<sup>29</sup>

As stated in an earlier paper (1917a), I trapped several years ago a mouse which I feel fairly certain was a juvenile yellow *gambeli*. It is possible that this character, in a heterozygous condition, may be of not uncommon occurrence among the mice of this vicinity. Thus, the mutation through which my stock came into existence may have taken place among the wild ancestors, many generations earlier. On the other hand, the same genetic instability which led to such a factorial loss or modification in one case may be responsible for its occurrence on many independent occasions. I have no data by which to decide between these two alternatives.

As regards the genetic behavior of these yellow mice, I have fairly satisfactory evidence that they are simple Mendelian recessives. As was stated above, 7 yellows and 14 normal animals constituted the fraternities in which they first appeared. The departure from Mendelian expectation may well have been accidental here, though a differential mortality may possibly have been responsible. The first yellows, bred to their (presumably heterozygous) parents, have given 5 dark and 5 yellow offspring. Bred to homozygous dark animals, they have thus far produced only a single brood, consisting of three dark individuals. Yellows bred to yellows have produced young of the aberrant type only (thus far 10). These frequently do not attain the full yellow color until they as-

<sup>29</sup> Mr. H. H. Collins has, however, found a number of sports of this general appearance among the offspring of a single pair of normally colored individuals which were trapped at La Jolla. Mr. Collins' mice differ somewhat in shade, however, from my "yellows," and may represent a distinct "mutation." His experiments have not been carried far enough to test the genetic behavior of this character.

sume the mature pelage, but I no longer have reason to doubt that the yellow type "breeds true."

A yellow female *gambeli* mated to a "pallid" male of the strain discussed above, has given birth to a single offspring, having abundant dark pigment in the skin, eyes and hair. In other words, these two pale, recessive mutants seem to be "complementary" to one another, as were Castle's two yellow races of rats (Castle and Wright, 1915).

### 3. *Discontinuous Variation in Restricted Pigment Areas.*

I have discussed briefly elsewhere several sorts of color markings, along with limited data which seemed to show that some of these were inherited in alternative fashion. Other characters of the same type have been added to the list. For example, in the second cage-born generation of *gambeli* I have found three mice with faces strongly "grizzled" by the presence of white hairs. It is probably no mere coincidence that these three grizzled specimens, while not belonging to a single fraternity, are all descended from the same grandparents. Neither the parents nor the grandparents were recorded as having the peculiarity in question, which would hardly have been overlooked if present. Furthermore, the single offspring which I have obtained from a "grizzled" pair exhibits this character plainly, though in a reduced degree. One specimen showing the white-faced condition likewise appeared in the C<sub>2</sub> generation of *sonoriensis*.

Again, occasional mice of perhaps all of the races are characterized by having considerable pigment in the skin of the tail. Normally, the skin of this member is nearly or quite devoid of pigment, the dorsal tail-stripe being due to black hairs. Examination of two successive generations of *rubidus* makes it probable that this caudal skin pigmentation is likewise a hereditary character.

I shall here discuss only one of the localized pigment variations which were dealt with in my earlier report on color "mutations." This is the occurrence of a white-tipped snout, due partly to the absence of skin pigment and partly to the presence in this region of white hairs.



I am now able to indicate rather more definitely the mode of transmission of this character. I wish to lay some stress here upon its genetic behavior, since I regard it as an interesting case in its bearings upon certain theoretical questions.

The pale-nosed condition has been studied only in the darkest of my races, *rubidus*. It was not noticed in the original wild stock, but it may well have been overlooked, as it is not a conspicuous character, and I was not searching for this type of variations when the wild generation was examined. In the first cage-born ("C<sub>1</sub>") generation twelve mice were recorded as having white-tipped snouts, four of the cases being entered as doubtful. At the time of examining these animals I had no idea as to the parentage of the individuals, so that there was no bias in my selection. Upon looking up their pedigrees, I found that ten of the twelve cases (eight certain and two doubtful) were the offspring (indeed, the *only* offspring) of two mothers of the wild generation (P ♀ 40 and 41) by a single father (P ♂ 15). The other two cases (both doubtful) were of other parentage. In connection with the figures just given, it must be stated that the C<sub>1</sub> generation consisted altogether of 60 (surviving) individuals, these being the progeny of twelve females and nine males.

Only 38 mice were obtained in the C<sub>2</sub> generation, 6 of which had white-tipped snouts. As before, the count was made without my being aware of the parentage of the individuals examined. Of the six "mutants," it turned out that four belonged to a fraternity of five, the fifth member of which was normal. This fraternity was the offspring of C<sub>1</sub> ♀ 61 (normal) by C<sub>1</sub> ♂ 10 (white-nosed). The other two mutants were the offspring of this same C<sub>1</sub> ♀ 61, by one of her brothers (♂ 3), the latter being likewise normally pigmented. These parent animals we may believe to have been heterozygous.

Unfortunately, none of the matings of the pale-nosed C<sub>1</sub> individuals *inter se* proved fertile, and indeed the only one of these aberrant mice which left descendants was the ♂ 10 referred to above.

The relationships here indicated, and the incidence of

the aberrant condition, are quite intelligible on the assumption that we have to do with a monohybrid recessive character. The character can not be dominant, for we had a case of white-nosed young from two dark-nosed parents. It can not well be due to more than one factor, owing to the relatively large number of recessive individuals.

#### VIII. DISCUSSION

Any one approaching the data dealt with in the foregoing pages, unhampered by theoretical considerations, would, I think, conclude that we had to do with two types of variation and two types of inheritance, differing from one another in rather fundamental ways. In the one class we have the continuously graduated differences, occurring within the limits of one of our "subspecies," as well as the differences in average or modal condition which distinguish the various subspecies from one another. Here we find a sensible *continuity*, both within and between these rather artificial assemblages of individuals, and distinct taxonomic units can be recognized only if we erect more or less arbitrary boundaries. In heredity, likewise, we have no indication of a dominance of one step or grade in this series over another, and little to suggest that two of these grades, once united or blended in the offspring, tend to reassert their independence in subsequent generations.

In the other class we have the "sports" or "mutations." These are distinctly *discontinuous*, in relation to the parent stock, either in the sense that one of the two possesses elements which are altogether lacking in the other, or at least in the sense that the new form has undergone such a change in the proportions of existing elements that its range of variation does not overlap that of the normal race. Looked at in another light, it is of interest to note that all the mutations which I have discussed, with a single exception, are dependent upon the loss of something. The red-eyed "pallid" mice have lost most of their black and some of their yellow pigment, the "yellows" have lost much of their black. The white-tipped tails are due to a loss of part of the dorsal tail-stripe, the

"grizzled" heads likewise to the local loss of hair pigment, while the white snouts have resulted from a loss of pigment both in the skin and hair of the latter region. The single exception among the "mutations" which I have observed in *Peromyscus* is the occasional presence of skin pigment in the tail. Here something has been definitely added to the usual condition.<sup>30</sup>

In heredity, too, these mutant characters, whether negative or positive, behave in distinctly discontinuous fashion. They do not blend, but are either present or absent in their entirety.

Taken at face value, I say, the evidence shows that we have to do here with two different types of variation and two different types of heredity. Now admittedly, the naïve view of such a situation is not necessarily the correct one, else we should be forced to return to the geocentric theory of the solar system. But even in this last instance, the burden of proof most assuredly rested on the man who first asserted that the sun did not move around the earth. And to-day the same burden rests upon those who claim—possibly with truth—that heritable variations are all discontinuous and that blended inheritance is an illusion.

In the few remaining pages of this paper, it is obviously impossible to discuss the various lines of evidence which have been advanced in favor of the Mendelian-mutation-pure-line scheme of things. I think that few would be enthusiastic enough to assert that the case had yet been really proved on evidential grounds. The considerations which are chiefly effective in determining one's adherence to this system of beliefs are doubtless of a more general nature. Thus it is argued that Mendelian inheritance has been shown to hold rigidly throughout a vast range of material, and that, therefore, the "unit-factor" conception is probably of universal application. Or, it is contended that the scheme of things here considered is more

<sup>30</sup> Even in this case, it is possible that we have to do merely with a "reversion," or return to an ancestral condition. Some other Muridæ (e. g., *Mus musculus*) normally have abundant pigment throughout the skin of their tails.

in harmony with the atomistic principles of physics and chemistry. "Unit-factors" have even been identified with molecules.

In respect to the pigmental characters of our geographic races, it has been shown to be probable that insensible gradations occur throughout considerable ranges of territory. There results a series in which marked contrasts can be found only by comparing individuals from widely separated localities. The hypothesis that the variations in this case are of the Mendelian type involves the assumption that the subspecific differences have arisen by a whole succession of small mutations in the same direction, the number of these mutations being a function of the distance from some hypothetical center of dispersal. In a recent paper (1917) Morgan has considered the question whether there are "any connections between the gradations of character in allelomorphic series and the order in which the characters appear," *i. e.*, whether "the assumed fluctuation of factors is a sequential process." He concludes that, "as a matter of fact, there is no such relation known . . . for the actual evidence from multiple allelomorphs shows that genes may mutate in all directions and also that extreme mutations such as white eyes arise suddenly from red and not by graded steps" (p. 524). These assertions, which, it is true, were primarily concerned with the effects of selection, lend little support to the view that graded geographic variations have arisen through mutation.

The attempt to explain away the substantial mass of evidence for permanent gametic blending and the indefinite efficacy of selection by invoking the theory of "multiple factors" is too well known to be reviewed here. Castle has been the most able and vigorous opponent of this theory. At present I will merely refer to certain evidence of my own which, I think, supports such an explanation no better than Castle's.

The dorsal tail-stripe is entirely lacking in a certain strain of my mutants. This stripeless condition is recessive to the striped one. In crosses with normal mice, the

stripe appears in its full size and intensity.<sup>31</sup> Nevertheless, the stripe itself was shown in the preceding pages to vary from race to race and from one individual to another. *And these variations, both racial and individual, were found to be hereditary.*

The case, of course, is parallel to that of Castle's hooded rats. Since "hoodedness" is recessive to "self-color" and reappears in one fourth of the  $F_2$  generation, Castle argues that it is dependent upon a single unit factor. Nevertheless, this factor itself presents hereditary variations in "potency," since it can be modified indefinitely by selection. The Mendelian counter-argument is that "hoodedness" behaves as a unit character in certain crosses merely because there is some one factor without which it can not manifest itself *at all*. The variability in its *degree of manifestation* is due to the fact that the hooded pattern is modified by the action of a number of independent cumulative factors. The argument seems a bit scholastic, but we must admit that it is logical and consistent.

Take another instance. Here I admit that my evidence is to some extent inferential at present. I have given good grounds for believing that the pigmentless condition of the snout in certain strains of *rubidus* is a simple recessive trait, dependent upon a single factor (or its absence). By this I mean that the pigmentless condition is probably allelomorphic to *any degree of pigmentation whatever*.

Now we find, in examining a series of mice, all gradations from those with heavily pigmented snouts to those in which no pigment is to be discovered with the aid of a hand lens. Indeed, there are a few "borderland" cases, which can be only doubtfully distinguished as pigmented or unpigmented. Unfortunately, I have no data showing whether or not these various gradations are hereditary. Analogy with the case of the tail-stripe would make it probable that they are. Moreover, we do know that those

<sup>31</sup> The fact that this condition of the tail stripe is but one manifestation of a mutation which has affected the hair pigment of the entire body does not affect the argument. It is generally believed that most "unit factors" manifest themselves in diverse ways.

differences in the mean condition of the snout which distinguish the various local races from one another are hereditary.

Here, too, I am aware that we could argue, with flawless logic, that the pigmentless condition was due to the dropping out of some single factor, without which the formation of snout pigment in *any* quantity was impossible. Each member of the graded series of pigmented snouts we might suppose to be conditioned by the presence of this color factor, together with one to many cumulative factors determining the degree of its manifestation.

Johannsen (1913), Morgan (1915) and others have made much of the increased range of variability which has frequently been met with in the  $F_2$  and subsequent generations, even when appearances otherwise pointed to a permanent blending of types. Recently several writers, particularly MacDowell (1916) and Little (1917), have analyzed some of Castle's data and have reached conclusions directly opposed to his. All of these authors (Castle excepted) hold that increasing range of variability in successive hybrid generations is strong evidence for the hypothesis of multiple factors, and we must grant that a pretty good case can be made out along these lines. The theory runs smoothly until we encounter the awkward class of facts which Johannsen has called by the name of "transgressive splitting," *i. e.*, the ultimate extension of the range of hybrid variability beyond that of both of the parent races combined. These facts would seem to prove too much, despite the ingenious explanation which has been offered by the pan-Mendelians to account for them.

An analysis of my quite limited data furnishes no evidence of an increased variability in the  $F_2$  generation, except where it pretty plainly results from an increase in the amount of actual abnormality, due to the conditions of captivity. In the largest, as well as the most normal of the series, the range of variation actually diminishes when we pass from the  $F_1$  to the  $F_2$  generation. I do not, however, offer the present evidence as conclusive, even for the single case of subspecific hybridization in *Peromyscus*. It should be confirmed by data derived from

more extensive series, consisting of animals which are free from any pathological modifications.

We must urge in passing, however, that evidence of segregation, even if valid, is not necessarily to be accepted as evidence of *complete* segregation. There is no reason why we might not have *partial* segregation, combined with partial gametic blending, as Castle maintains.

In two recent illuminating articles (1917, 1917a), Jennings points out how Mendelian-mutationists of the most extreme school have been driven by their own researches into a position that does not differ, according to any pragmatic test, from the one which they so long have vehemently opposed. More and ever more minute hereditary differences in the manifestation of a given character are recognized, until the limit of distinguishability is approached. This state of affairs has been attributed to two causes: (1) hereditary modifications in the constitution of single factors, resulting in the formation of series of gradations, allelomorphic to one another; and (2) the existence of series of independent modifying factors, cumulative in their effects.

As remarked earlier in this paper, the contest has latterly come to resemble that allegorical one of the two knights, fighting upon the opposite sides of the same bi-colored shield. And yet there would seem to be a difference. The two knights in the legend were both equally right. In the present case, if we may judge by every pragmatic consideration, the larger measure of right belongs to those who have contended for the frequent permanent blending of hereditary characters in crossing and the continuous modifiability of these characters through selection. The finely spun theories of their opponents may help us to symbolize the machinery underlying these phenomena, but the phenomena themselves, and not the theories, are the indubitable realities in the case.

#### IX. SUMMARY

1. In the preceding pages, the differences, structural and pigmental, which distinguish four geographical races of deer-mice are discussed in some detail. The pigmental



differences relate to a considerable range of more or less independently varying characters, affecting both the intensity and the extensity of the pigment in the hair and skin. They are found to be, in a general way, correlated with certain elements of the physical environment, while the structural differences do not appear to be so correlated.

2. All of these differences, structural and pigmental, are found to be differences of degree, revealed through a comparison of mean or modal conditions rather than of individual animals. In comparing the less divergent of these races with one another, the frequency polygons for any given character overlap broadly.

3. These subspecific differences, and even the minor differences which distinguish one narrowly localized sub-race from the parent form, are found to be hereditary, as evidenced by their persistence when environmental conditions are interchanged.

4. The gradations in certain of these characters by which individuals of the same race differ from one another are found to be strongly hereditary.

5. Hybrids between even the most divergent of these four races are predominantly intermediate in character, both in the  $F_1$  and the  $F_2$  generations. In both of these generations a wide range of variability is exhibited, which, however, is little if any greater in the  $F_2$  than in the  $F_1$ .

6. In contrast to the sensibly continuous variation and sensibly blended inheritance shown in respect to these subspecific characters, is the behavior of certain "mutations." Here we meet with typical discontinuous variation, and inheritance of the strictly alternative or Mendelian type. It is insisted that the burden of proof rests upon those who contend that these two types of variation and inheritance are reducible to a single category, that of discontinuity. Anything like a proof of this contention appears to be thus far lacking.

#### SUPPLEMENTARY NOTE (JULY 23, 1918).

It gives me pleasure to call attention to points of close similarity between certain of the views expressed in the



foregoing pages and ones which have recently been advanced by Gates (1917) and by Goldschmidt (1918); likewise to the resemblance between some of the features of geographic variation which I have described for *Peromyscus* and those which have been observed by Swarth (1918) for certain birds. None of these articles had been published at the time the present paper was written.

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## JOAN BAPTISTA PORTA

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LIKE a cemetery with costly monuments for the rich, modest wooden crosses for the poor, and for others sites unmarked, hidden beneath brambles and weeds, a picture of death and oblivion—so history of botany has dealt with records of the past, with life and labors crowned with success or hopelessly ignored and forgotten.

For years, nay centuries unchallenged some works have braved the everchanging hands of time, guiding human thought into a highway with increasing light, confronting nature, its laws and problems; great steps have been taken forwards, new facts have been born, militating against former, old conceptions and resulting in complete revolution. Coupled with intense sincerity great skill has conquered, paving the way for future research, culminating in success, or suddenly, without a warning, crushed with defeat. Many a brilliant thought, but disguised by a less powerful style, has remained obscure and unnoticed, until at some proper time, as if surviving itself, it has arisen and gained due homage, even though late and in foreign soil.

Inclement fate has doomed to silence names of great men, more fortunate thus than labors of merit that have been misunderstood, carelessly weighed, and exposed in unfavorable light. Who knows Porta? His work was soon forgotten and in history it stands among those ridiculed or silently passed by. He was born in classic Italy, in the middle of the sixteenth century, an era of scientific research, marked by rapidly increasing interest in botany, with splendid results laid down in precious volumes, copiously and carefully illustrated. They were the days of Cæsalpino, Dodonæus, Conrad Gesner, Fuchs, Clusius,

Lobelius, Caspar Bauhin, all workers in botany, seeking the same source for solving the problems of the plant world, through demonstrating the relations between the plants themselves, and beginning with classification first of all. At that time literature was less than scant; there was actually nothing to distract the views of investigators; it was an era of thought original, with room only for the gifted and talented, none for the mediocre. And strange to say, Cæsalpino, though secluded from the botanical centers of Holland, France, and Germany, rose to hold the palm as the most brilliant of his contemporaries. In modern times he is still revered as the father of systematic botany. To these men Porta was not known, and presumably they were not known to him either. To describe the principal episodes in the life of Porta, the various phases of his character and labor, history has little to say, fame less.

He was born in Naples, in the year 1545, and he did succeed in gaining reputation as a noted naturalist, philosopher, physician and pharmacologist. His home was a favorite gathering place for men of learning; meetings were held, dubbed "*Accademia dei Secreti*," and themes were discussed delving into all the mysteries of nature, principally the chimerical secrets of magic. That Porta held an eminent place among his associates seems proven by the fact that they regarded him as "a new prophet," and as such Porta was summoned to the court of Rome to defend himself. He must have made a bold stand, for instead of meting out some punishment for his suspected, supernatural power, the court exonerated him and elected him a member of the *Accademia dei Lincei*. After that time he lived in Rome for several years, and he died in February 1615. The only botanical work written by Porta is "*Phytognomonica*," published in Naples, 1588. Three subsequent editions, 1591, 1608, and 1650, were published in Germany. In the later years of his life Porta acquired no small notoriety as an author of dramas and tragedies. Considering the profuse material treated in "*Phytognomonica*," and the fact that Porta was only in

his forty-fourth year when the work appeared in print, he must have begun his botanical career at a very early age.

In this work, "Phytognomonica," Porta introduced a new system for plants, but far different from those established by his contemporaries or predecessors. His mind, evilly influenced by the extravagancies of the Paracelsistes, dwelt mostly upon such singular phases, remote from natural history, as similarity between parts of plants and organs of man and animals, or the resemblance of parts of plants with diseases of man and animals, furthermore the habit or aspect of plants as being analogous to those of man, and finally the relation of plants to the stars, the sun, and the moon. Nevertheless Porta was a botanist, and a very learned one. His studies of plants reveal more than a superficial knowledge of their parts, and he must have known many. But from beginning to end the system, or better the method, proposed by him was too enigmatic to conform with the requirements of natural science, founded as it was on principles so contrary to nature as they possibly could be; and so the system never reached beyond being considered the product of "l'imagination brillante mais déréglée."<sup>1</sup>

It is, indeed, difficult to understand how a man so intellectually gifted as Porta would ever waste his time and labor on such problems as to demonstrate the secret virtues of plants by merely observing the forms of their parts and the color of their flowers. Thus according to Porta certain species of *Orchis* with the roots palmate, and grasses with the spikes in fives (*Cynodon Dactylon*) would be a safe remedy for diseases in foot or hand, for gout, etc.; plants with heartshaped roots or fruits (*Valeriana*, *Persea*) for heart disease; plants with the flowers resembling eyes (*Aster*, *Sedum*) for eye diseases. Furthermore, plants with spotted stems (*Araceæ*) would on account of their likeness to snake-skin be useful as

<sup>1</sup> Compare Planchon, J. E., "Des limites de la concordance entre les formes, la structure, les affinités des plantes et leurs propriétés médicinales," Thèse, Montpellier, 1851.

antidote for snake bites, etc. Forty-two sections of this type are described by Porta, and some are fairly well illustrated. Much attention is given to citing and explaining descriptions and names of species known to and mentioned by the old authors, Pliny, Dioscorides, Columella, and others, and from this particular viewpoint the book is quite interesting and useful.

But even if the greater part of this book is devoted to considerations of the secret virtues of plants, some chapters and remarks, scattered here and there, reveal the indisputable talent of Porta as an observer of plant life. To do full justice to this part of his work let us briefly consider the status of botany in the sixteenth century. It was an era of classification or attempted classification; the plants were described and arranged in some way as an expression of their mutual relationship. By Bock (1560) they were divided into herbs, shrubs, and trees; by Clusius (1576) the system became enlarged so as to comprise bulbous plants, plants with the flower fragrant or inodorous, plants with milky juice, etc. The descriptions furnished by Clusius have always been regarded as most excellent, but he gave much more attention to the foliar structure than to the floral; in this point of view he was followed by Lobelius and Dodonæus. Caspar Bauhin (1550-1624) established a system covering twelve books, and he began with the grasses and grass-like plants, including *Iris*, *Acorus*, etc.; after these came the bulbous plants, then those with large, edible roots, etc.; the genera were not described, only the species with a number of synonyms. Bauhin was the earliest author to use binary names; but in describing the plants he did not consider the structure of the flower, nor the fruit. Finally Cæsalpino (1583) not only established a system principally based upon the organs of fructification, hitherto ignored, but he added a large number of new observations of great importance to the study of botany. The introduction to his work contains a discussion of theoretical botany in general. With regard to his classification of the plants, into arborescent and herbaceous, the

minor groups, characterized by the structure of fruit and seed, are not natural, except the sixth, which comprises the Umbelliferae, the tenth, Boragineae and Labiatae, and the fifteenth, plants destitute of flowers and fruits, ferns, mosses, and fungi.

Naturally the tendency to classify governed botanical research during as early a period as the sixteenth century, and the various systems proposed were all purely artificial. Not until the year 1703 were the Phanerogams distinguished as mono- and dicotyledonous by Ray. We remember that so late as the middle of the eighteenth century Linné established his artificial system, based upon the floral structure, and at about the same time Antoine Laurent de Jussieu undertook the task to describe the families. In other words, Bauhin wrote the diagnoses of the species, Tournefort (about 1700) characterized the genera, Linné arranged the genera in groups, which he named only, and finally Jussieu established a natural system with family-diagnoses. But returning to the sixteenth century, the actual knowledge of the plants was embodied in systems, and beyond the mere classification no attempts were made to consider the plants from a biological viewpoint, as members of a living world adapted to environments of highly different nature as to climate and soil, at least not in accordance with the history of botany. The treatment of this particular phase of plant life was reserved to the very close of the nineteenth century, when Warming<sup>2</sup> introduced a supposed new branch of botanical science, dealing with plant societies, now universally recognized as plant ecology. The appearance of this work has brought about a fuller valuation of the factors that govern plant life, a purely biologic consideration of the plants on morphological and physiological grounds. However, twenty years of experience has taught us that this branch of botanical science lacks organization and is yet rather to be compared with a speculation having run far in advance of facts. Nevertheless the supposed new doctrine

<sup>2</sup> "Plantasamfund," Kjøbenhavn, 1895.

does exist, and has existed for more than three centuries, founded by Porta, and amply discussed in several chapters of his "Phytognomonica." No mention is made by Warming of Porta's book. And, strange to say, no mention is made of Planchon's either. By Sachs<sup>3</sup> Porta is passed by in silence.

Planchon (*l. c.*), Guy de la Brosse<sup>4</sup> and Adanson<sup>5</sup> refer only to the part dealing with the secret virtues of plants; the chapters on plant societies are ignored, or let us say not appreciated.

To Porta the method of classifying plants as instituted by his contemporaries must have been absolutely unknown; of rendering the knowledge of plants more accessible by means of a system he had no thought. His principal object was to demonstrate the virtues or properties possessed by plants, and, as stated above, Porta combined these with the general aspect of plants, the shape of their leaves, stems, etc. While making these observations in the field, as he did, Porta became aware of the distribution of a number of species under conditions very variable, and especially with regard to the soil. He noticed the fact that the general aspect of the plants, their shape, color, odor, hairiness or smoothness, at least to some extent, depended upon the environment in which they grew, and from this point of view, we might say "biologic," did Porta elaborate the introduction to his "Phytognomonica." He divided the plants in two groups, aquatic and terrestrial, each with several subdivisions. Of the former, examples are given of species characteristic of lakes, swamps, rivers, brackish marshes, etc., and he described the habit of several plants, in most cases very correctly. With respect to the terrestrial plants Porta distinguished between those that occupy a rich, a dry, or a sandy soil, illustrated by *Malva*, *Lithospermum*, and *Fæniculum*. Furthermore, some amphibious species are described, such as are terrestrial but

<sup>3</sup> "Geschichte der Botanik," München, 1875.

<sup>4</sup> "De la nature des plantes."

<sup>5</sup> "Familles des plantes," Vol. I, préf., p. ii, 1763.



adapted also to live in the water. In several chapters descriptions are given of the habits of plants, of species characteristic of the mountains, the lowlands, the hill-sides, and the shady valleys; to these were added some brief remarks upon the vegetation of the northern, the temperate, and the torrid zones. Among the cultivated plants Porta mentions *Zea*, which, however, is not the plant known now under this name (maize), but a kind of wheat (*Triticum Spelta*) as demonstrated by De Candolle. In bringing these facts together Porta certainly laid the foundation of plant ecology, and the classification, proposed by Warming (*l. c.*), of the various plant societies: "*Hydrophytes*, *Xerophytes*, *Halophytes* and *Mesophytes*" is not much more instructive than the one introduced by Porta: "*plantæ palustres*, *fluviales*, *marinæ*, *salsæ aquæ*, *silvestres*," etc.

Naturally these groups have received a more elaborate treatment by authors of a recent date, especially with reference to the internal structure, which often, but very far from always, is in correlation with the respective environment. However, the weakness of modern ecology rests on the belief that the structures may be explained as caused by the natural surroundings. Experience has taught that the genera and species do possess some character of their own, which they never give up. To a certain limit the plants may allow themselves to submit to changes, but beyond that they will sooner die.

So far as Porta considered the biologic question of plant life, dealing only with the superficial aspect, more or less comparable to the surroundings, he committed no errors of consequence. For as a matter of fact the principal features exhibited by members of plant societies are mainly external, such as the shape of leaves, their relative size, the organs of vegetative reproduction, and the general habit; the internal structure cannot be relied upon, at least not at the present stage of our knowledge of plant life.

Thus already in the sixteenth century the first essay on plant ecology appeared, and Porta was the author.

## SHORTER ARTICLES AND DISCUSSION

### AN AUTOSOMAL BRISTLE MODIFIER, AFFECTING A SEX-LINKED CHARACTER

A RECESSIVE gene in the third chromosome of *Drosophila melanogaster* (*ampelophila*) affects the bristles on the thorax and scutellum of females which are heterozygous for a recessive sex-linked character, forked in such a way as to make forked semi-dominant. This latter character has been described by Morgan and Bridges (Carnegie Publ. 237). The bristles of "stock" forked flies are shortened, twisted, and heavier than normal. This applies to the bristles of the head, thorax and scutellum. Flies heterozygous for forked, that is, females, since the gene is in the X chromosome, have normal bristles unless the fly is also homozygous for the third chromosome modifier here recorded. Females with one forked gene and one normal allelomorph, which are homozygous for a modifying gene in the third chromosome, are intermediate in appearance between forked and normal flies, and are designated as "semiforked." The males never show the character since they are never heterozygous for sex-linked factors. The forked appearance is limited to a few of the thoracic and scutellar bristles and the bristles in general are less affected than are those of the homozygous forked flies as regards thickening of bristles and twisting. Both of the third chromosomes must bear the modifying gene in order to affect the bristles. In the absence of the forked gene, the semiforked genes, even when homozygous, are nearly always without effect, but occasionally a few individuals may be detected which have shorter and heavier bristles, but this is not pronounced and is rarely found. Flies which are known to be pure both for forked and for the modifier, semiforked, can not be distinguished from the simple forked individuals without the modifier.

#### ORIGIN OF SEMIFORKED

The semiforked character was first observed in February, 1918, in the heterozygous Bar forked daughters resulting from culture 668, a cross of a Bar male from stock to a forked female of a non-disjunction strain which had been used to observe non-

disjunction for about three months previous to this mating. The semiforked females were not noticed until the bottle was half through hatching, probably being overlooked. The counts show that after the new character was found there were 15 such females and 42 of the expected normal bristle type. This is clearly a 3:1 ratio and both parents must have been heterozygous for the semiforked gene. Although they were not brother and sister, this is not improbable, because the gene seems to have existed originally in the Bar stock, which, however, was not pure for it. The forked female doubtless obtained the gene from the Bar stock also, as her pedigree contains many Bar stock males used in the non-disjunction experiments. Since attention was paid only to the behavior of the X chromosomes, it is easy to see that the autosomes would be interchanged from generation to generation and the forked female could have a third chromosome which came originally from the Bar stock.

The strain was kept going by brother-sister matings. One  $F_2$  culture (712) of a forked male to a heterozygous Bar forked female, which was semiforked, produced all the heterozygous forked females with semiforked bristles. Here both parents were pure for the modifier. In Culture 722, which was an  $F_2$  from 668, half of the females heterozygous for forked were semiforked. In this case, one parent was pure and the other heterozygous for the modifier. One case was observed where a forked male crossed to a semiforked female produced no semiforked daughters. The explanation is that both the third chromosomes of the father carried the normal genes. The reverse case of this was shown when a forked male was crossed to a heterozygous Bar forked female with normal bristles. Of the heterozygous forked females produced, approximately half were semiforked and half normal bristled. Here the father was pure for the modifier but the mother was heterozygous for it and the 1:1 ratio resulted.

#### LOCATION OF MODIFIER

The presence of the modifying gene in the third chromosome was demonstrated by the following method, which has been used before in work on *Drosophila*. A semiforked female was outcrossed to a star dichæte male from stock. Forked star dichæte males were selected from the offspring and back-crossed to the semiforked females from stock cultures. Star and dichæte are dominants in the second and third chromosomes respectively

and are used because they can be easily detected in the heterozygous condition. Since there is no crossing over in the male in *melanogaster*, any dichæte fly in the offspring of the back-cross must have obtained one third chromosome from the dichæte stock and one from the semiforked stock. Any fly which was not dichæte traces back both its third chromosomes to the semiforked stock.

Examination of the offspring from the back-cross in three cultures showed that no dichæte fly was ever semiforked and, conversely, all not-dichæte females were semiforked, provided they were heterozygous for forked, and this includes all those not homozygous forked. About 500 individuals were obtained from these three cultures and the above statement is based upon them. The result is absolutely clear-cut and shows that the modifying factor is recessive and in the third chromosome. The presence of the star chromosome (II) did not affect the appearance of the semiforked character in any way. The location of the gene within the chromosome by its linkage relations to other third chromosome genes has not been carried out.

#### SUMMARY

1. A recessive third chromosome modifying gene converts heterozygous forked females into intermediate semiforked individuals.
2. Homozygous forked flies are not visibly affected by the modifier.
3. The semiforked modifier rarely produces any visible effect when homozygous unless the forked gene is present.

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